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PALAEONTOLOGIA AFRICANA

ANNALS OF THE BERNARD PRICE INSTITUTE FOR
PALAEONTOLOGICAL RESEARCH
UNIVERSITY OF THE WITWATERSRAND
JOHANNESBURG

VOLUME 17, 1974

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VOLUME 17, 1974

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BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH

1974

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BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH, UNIVERSITY OF THE WITWATERSRAND, JOHANNESBURG
REPORT OF THE HONORARY DIRECTOR (Dr. S. H. HAUGHTON) FOR THE CALENDAR YEAR 1973

At an official University function on the afternoon of 14 February, 1973, the extensions to the Douglas Smit House, which is the Institute's headquarters, were opened by the President of the Council for Scientific and Industrial Research, Dr. C. van der Merwe Brink, in the presence of some two hundred invited persons including the Vice-Chancellor and Mrs. Bozzoli. Dr. Brink was introduced to the assembly by Dr. F. G. Hill, and thanked for his action by the Honorary Director of the Institute.

These considerable extensions now afford opportunities for additional public displays of representative fossil material with which the Institute is concerned, for very much greater storage accommodation for the rapidly growing collections which are the basis of its scientific studies, and for much more comfortable working conditions for members of both the scientific and technical staff and for the scientists from other organizations, local and foreign, who visit the Institute for study purposes. Space and equipment for University lectures and demonstrations to be given to postgraduate students have also been made available in a special lecture theatre. In addition, too, to providing space for the work of its permanent staff and for that of visiting scientists, the Institute is now able to grant free accommodation to several persons who are completely supported financially by the Johannesburg-based companies Anglo American Corporation and Soekor. Three of these persons are postgraduates preparing theses for higher University degrees; but Soekor has increased its staff working in the Institute by two European girl assistants and four African preparators.

Dr. H. Tralau, of Stockholm, who had been officially appointed to succeed Dr. Edna Plumstead as senior staff palaeobotanist, decided early in the year, after a delay of several months, that he was refusing to accept the appointment and the post is thus vacant and has had to be re-advertised. The new advertisement produced no acceptable replies, and the University has decided not to seek other applications until towards the end of 1974. Fortunately, the advice and assistance of Dr. Edna P. Plumstead—who has been designated Honorary Research Fellow by the University after her official retirement from its staff—has been available for certain periods during the year.

STAFF MATTERS

The Assistant Director, Dr. A. R. I. Cruickshank, left for overseas on a period of study leave in the middle of August and is expected to return in the middle of February, 1974. Much of this leave was spent at the University of Newcastle-on-Tyne in the study of Mesozoic Fossil reptilia; but a visit to certain Museums in the United States of America will be included in his itinerary.

Dr. Cruickshank attended a Symposium on Vertebrate Palaeontology and Comparative Anatomy at the University of Leeds on 18th to 20th September, 1973. At this symposium he contributed a review of recent and current palaeontological studies in southern Africa. An informative report by him on the various papers read at the meeting has been received and circulated to staff members of the Institute.

At a University graduation ceremony in April, the degree Ph.D was conferred on Dr. J. W. Kitching, who has served the Institute since its inception. He was thereupon regraded by the University to a post of Senior Research Officer and, during Dr. Cruickshank's absence overseas, has fulfilled, with full satisfaction, the functions of Assistant Director. At its Annual General Meeting in Pretoria, the South African Association for the Advancement of Science elected Dr. Kitching to the Council of its Witwatersrand branch.

Mr. P. Nagel was appointed to a new post of Photographer-Technician at the beginning of the year.

Mrs. S. J. Holloway, for family reasons, left the post of Secretary-Typiste at the end of December after a period of very satisfactory service.

Miss Emanuel, desirous of undertaking further studies in Art, also resigned at the end of the year. She, too, had rendered yeoman service to the Institute during her years of service.

The appointment of a technician (Field Officer) to the staff was still outstanding at the end of the year.

On her retirement from service with the University Dr. Edna P. Plumstead was offered and accepted the title of Honorary Research Fellow for Palaeobotany in the Institute and was enabled, through the generosity of the C.S.I.R., to employ a part-time secretarial assistant. In the absence of a Senior Research Officer in Palaeobotany, she kindly agreed to act as supervisor of the work of Ph.D. candidates in her field, but found it impossible to continue as such in the case of Mr. J. Anderson, whose supervision was then assumed by Mr. R. Pienaar of the University's Department of Botany.

As President of the I.U.G.S Sub-Commission on Gondwana Geology, Dr. Plumstead attended the

Third International Symposium of this Sub-Commission which was held, under the sponsorship of the Australian Academy of Sciences, in Canberra, Australia from 20th to 25th August, 1973. From the 13th to the 17th of August she was present at the 45th ANZAAS Congress in Perth, Australia as the principal delegate from South Africa nominated by the C.S.I.R., at which a total of 5 200 delegates was registered as attending. She did not join any of the official excursions associated with the Gondwana symposium, preferring to spend time in visiting collections at the National Museum in Sydney, Newcastle, Brisbane, Melbourne, and Hobart and in field excursions to fossil plant occurrences under the guidance of experts, making collections, particularly of the *Glossopteris* flora, for subsequent transmission to the Institute. From the 9th to the 22nd of September she paid a private visit to New Zealand, mainly for the purpose of palaeobotanical studies, especially of the fossil plants collected in Antarctica. Dr. Plumstead, in a long report to the C.S.I.R., has expressed her deep appreciation of the friendly reception given to her by Australian and New Zealand fellow-workers.

In June, 1973, Dr. Plumstead received, from the hands of Dr. Haughton, the Honorary President for that year, the South African Medal of the South African Association for the Advancement of Science for her eminent work in the fields of palaeobotany and stratigraphy.

FIELD WORK

Most of the field work undertaken during the year under review consisted of short trips for the collection of fossils or made in company with visiting scientists for instructional purposes.

Dr. Cruickshank, prior to his overseas visit, spent one period of four days in Natal and one of the same length in the Douglas area with two of his research students, Miss A. Anderson and Mr. I. McLachlan, to study the problems and possibilities of collecting tracks and rather sparse invertebrates from the lower beds of the Karroo sequence. In May, he visited the South African Museum in Cape Town to study the dinosaurs there in connection with his research work on the ankles of archosaurs.

Dr. Kitching accompanied Dr. R. Carroll, a visiting paleontologist from Redpath Museum, McGill University, Canada on a visit to the Rubidge collection at Wellwood, Graaff-Reinet and to the Albany Museum in Grahamstown; from both of these collections a number of fossil reptile specimens were borrowed for study purposes and early return.

In July (17th—21st) he accompanied the film unit of the S.A. Broadcasting Corporation, which was working in preparation for their introduction of television, to the Harrismith area; while filming was in progress, he collected a number of well preserved skulls of *Lystrosaurus* and *Lydekkerina*. During short periodic visits to the Graaff-Reinet and Pearston areas he collected another 28 fossil reptilian skulls. For four days in October he accompanied four visiting Japanese geologists on a study of small areas in the Lower and Middle Beaufort beds of Harrismith and Bergville, where they collected a few *Lystrosaurus* skulls and skeletal elements, for which export permits have been obtained.

From Dr. Kitching's brother Mr. B. J. Kitching, stationed at Middelburg, Cape, on police duties, the Institute has received a donation of 12 skulls of *Lystrosaurus,* an almost complete skeleton of *Thrinaxodon* and four small therocephalian skulls with skeletal elements.

In connection with investigations which are being undertaken under the aegis of the Atomic Energy Board into uranium mineralization in Karroo sediments, Mr. B. R. Turner spent part of November and December on a sedimentological study of Lower Beaufort strata around Merweville, C.P. in order to establish current directions and environments of deposition. His observations have not as yet been finalized into report form. Mr. Turner also participated in an excursion from Bloemfontein, organized by the Karroo working group of the South African Commission for Stratigraphy which is examining the validity of proposals that have been made for the nomenclature of Karroo lithostratigraphic units.

Mrs. H. M. Anderson took leave from 13th March to 12th June, in order to study palaeobotanical collections in various centres in Germany, Switzerland, Denmark, Austria, France, and Great Britain and to consult literature in this field not available to her in South Africa, all in connection with a doctoral thesis on the fossil flora of the Molteno beds which she is preparing. In her examination of the European Triassic flora she was generously assisted by resident palaeobotanists and was particularly helped in specialised libraries in Frankfurt and Stockholm.

Mrs. Anderson organized and participated in a collecting trip to the Birds River fossil plant locality and to the Mooi River and Little Switzerland sites for Dr. B. Riek, an Australian expert on fossil insects. From Birds River a record number of 35 insect remains were obtained (which Dr. Riek is describing), as well as numerous good plant fossils, some Conchostraca, and a fossil fish.

Mrs. B. Maguire (formerly Miss J. M. Roets) collected bones from a series of porcupine lairs at the base of a cliff near Zebediela's Nek, the study of which will form an integral part of her doctoral thesis on fossil porcupines.

Mr. B. Maguire paid several visits to Makapansgat; but a considerable part of his time in the first half of the year was devoted to assisting Dr. Kitching in the transference of the Limeworks bone tool and faunal collections to the new museum and their arrangement in the museum.

Miss A. Anderson collected track-ways from various exposures of Dwyka and Ecca beds in the western part of the Republic.

Mr. I. R. McLachlan (a part-time Ph.D. student) continued his investigations on Karroo microfauna at various sites in the Western Cape, the Douglas area (C.P.), Gordonia (C.P.), Natal, and the Ermelo area of the Transvaal. He has utilized several different techniques for the processing of the rocks in the study of the contained microfaunas. He attended the Gondwana symposium in Canberra during August, 1973 as a delegate from Soekor and presented a paper, written jointly with Miss A. Anderson, entitled "The Marine Incursions into Southern Africa during Dwyka times".

Excavation and collection at the Sterkfontein caves, west of Johannesburg, was continued throughout the year. A squad of African labourers has operated systematically under the direction of Professor P. V. Tobias and Mr. Alan Hughes of the University Department of Anatomy. This "cave" site attracts a considerable number of public visitors, over whose activities strict control is necessary. The Board of Control has therefore authorized the preparation of a "Guide Book" for sale, the erection of notice boards, the employment of competent guides, and the preparation of automatically-operated audio aids.

RESEARCH WORK

The need for physical re-arrangements entailed by occupation of the completed additions to the Douglas Smit building, including an additional exhibition Hall which will be devoted to the display of Tertiary and Quaternary material, has detracted from the time available to certain staff members for pure research work, particularly in respect of the more senior members of the permanent staff. The Assistant Director, Dr. J. W. Kitching, and Mr. and Mrs. Maguire have had to spend a considerable time in dealing with administrative matters that arise daily and in the supervision and the actual transference of many thousands of specimens to their proper storage sites. A tribute must be paid to the enthusiastic manner in which the scientific workers as a body have undertaken this essential work of converting a "dump" of fossils into an orderly arranged collection of scientific material. With all this, however, research work has not been neglected.

Prior to going on leave, Dr. Cruickshank was busy on two projects. One of them is the anatomy of the Anomodonts of the Upper Beaufort beds and of the Triassic generally (particularly the genus *Kannemeyeria*); the other is the study of the ankles of diapsid archosaurs and the relationships of Sauropods and Prosauropods.

Dr. Kitching, in addition to preparing his Ph.D. thesis for publication, has found time to continue with descriptions and identifications of the fauna from the Cave of Hearths deposit and to study millipedes from the *Lystrosaurus* zone—a new discovery made by him.

Mr. B. R. Turner has been engaged on the statistical analysis of sedimentary cycles, with particular reference to those found in the Molteno succession. A method was devised for depicting cycles by a mathematical combination of grain size and bed thickness of sandstones in a succession. A paper on this method was submitted by him for publication to the *Journal of Sedimentary Petrology* in America and has been tentatively accepted subject to condensation and minor revision.

Mr. B. Maguire devoted most of the second half of the year to the preparation of his Ph.D. thesis, entitled "The Flora of Makapansgat and the Food Plants of Kalahari Bushmen with especial reference to the potential vegetable dietary of Living and Extinct Hominids". Preparation of this thesis has entailed many studies of the living flora in the northern half of the Republic and the Kalahari areas of Botswana and of the food habits of primitive Bushmen, together with the bearing of these observations on the probable habits of life of the fossil hominids of the Makapansgat cave deposits. These studies have been undertaken over a number of years.

Mr. C. E. Gow has completed his studies of the genera *Youngina* and *Prolacerta,* including that of most of the postcranial skeleton of a *Youngina.* Preparation of his Ph.D. thesis for submission is under way—all the drawings have been completed.

Mrs. H. M. Anderson, prior to her visit overseas, submitted a thesis on the fossil flora of the Molteno beds for examination. This, however, was considered by the appointed examiners to be unacceptable for the degree of Ph.D., and she has been requested to revise and extend her observations in order to meet the examiners' objections to the first submission. This she is doing.

Miss Ann Anderson, who is preparing a Ph.D. thesis on "Arthropod Trackways and other trace fossils from the Dwyka and Ecca series of South Africa", collaborated with Mr. I. R. McLachlan in the preparation of a paper recording the first unambiguous marine fossils to have been found in part of the Karroo basin. Twenty arthropod trackway localities—only half of which were previously recorded—have been selected for description and detailed mapping. The tracks found have been taxonomically classified and photographed (about 300 from the B.P.I.P.R. collection), and measurements taken of certain features within the various ichnogenera.

Miss S. Chernin, a Ph.D. student, is reviewing the South African fossil amphibia and expecting to simplify the confused taxonomy of the group that exists at present. She undertook a study trip to the South African Museum in Cape Town, taking some 200 photographs of specimens in its collection. She also borrowed from it an as yet unnamed,

exceptionally large but badly fragmented lower jaw which may prove to be the largest fossil amphibian ever found in South Africa. This she is now preparing by hand for study.

Mrs. J. Maguire has her doctoral thesis in an advanced stage of preparation, the subject being South African fossil porcupines. She intends to submit it in two volumes, the first devoted to the geology of the deposits and the taxonomy of the fossils, and the second to appendices (including porcupine ecology and bone accumulations) and references.

Miss G. E. Collings—an M.Sc. student—has selected the machaerodonts of South Africa as her field of study, and has completed her thesis.

Mr. I. R. McLachlan, a part-time Ph.D. student, spent time in field observations in both the N.W. Cape and in Natal. He particularly studied the gradation in Natal from the marine Dwyka shales into the Lower Ecca shales in which he found fossil wood and calcareous nodules containing siliceous sponge spicules. He is concentrating, in the laboratory, on the identification of microfossils from these lower horizons of the Karroo system. He also, through the generosity of his employer, Soekor, attended the Gondwana symposium at Canberra in August, contributing a paper entitled "The marine incursion into southern Africa during Dwyka times" written by himself and Miss A. Anderson.

Dr. E. P. Plumstead spent much of her available time in the Institute on her major project, which is a detailed description of the Glossopteridophyta, a division of the late Palaeozoic—early Mesozoic plants that occurs in several separate parts of Gondwanaland. She agreed to continue as supervisor for four research students in palaeobotany who are registered with the University—Mrs. H. Anderson, Mrs. A. Malleson, Mrs. R. Falcon, and Mrs. S. Smithies.

Dr. C. Mendrez of Paris, a Ph.D. candidate, who suffered the loss of much of her manuscript and illustrations by theft in Kimberley in June, 1972, spent some time in the Republic in an endeavour to complete her "Review of the Whaitsiidae, mammal-like Reptiles from South Africa, Tanzania and Russia" working in the Institute, at Wellwood (Rubidge collection) and in the South African Museum. She intends to visit the country again in 1974 in order to complete her thesis. She has completed a paper on *Promoschorhynchus* for ultimate publication by us.

LECTURES

The following members of staff have lectured to undergraduate students and supervised practical classes in the University's Department of Geology: Dr. A. R. I. Cruickshank, Dr. J. W. Kitching, Mr. B. R. Turner, Mr. C. E. Gow, Mrs. J. Maguire, and Mrs. H. Anderson. Several mid-day lectures were arranged within the Institute, given by staff members and by visiting palaeontologists. Examination papers were prepared by all the members of staff here named.

PUBLICATIONS

During the year three issues of *Palaeontologia Africana* appeared—Part 1 and Part 2 of Volume 15 and Volume 16. The individual contributions are as listed here.

Vol. 15, Part I

1. McLachlan, I. R. Problematic Microfossils from the Lower Karroo Beds in South Africa.
2. Eriksson, K. A. and Truswell, J. F. High Inheritance Elongate Stromatolitic Mounds from the Transvaal Dolomite.
3. Forey, P. and Gardiner, B. G. A new Dictyopygid from the Cave Sandstone of Lesotho, Southern Africa.
4. Gardiner, B. G. New Palaeozoic Fish Remains from Southern Africa.

Vol. 15, Part II

1. McLachlan, I. R. and Anderson, Ann. A review of the Evidence for Marine Conditions in Southern Africa during Dwyka times.
2. Cruickshank, A. R. I. The Mode of Life of Gorgonopsians.

Vol. 16

1. Haughton, S. H. Report of the Honorary Director for the year 1972.
2. Keyser, A. W. A new Triassic Vertebrate Fauna from South West Africa.
3. Jubb, R. A. Brief Synthesis of Present Information on the geographical and stratigraphical distribution of Fossil Fish within the Stormberg Series, South Africa.
4. Keyser, A. W. A re-evaluation of the genus *Tropidostoma* Seeley.
5. Marguerier, J. Paleoxylologie du Gondwana Africain; Etude et Affinités du genre *Australoxylon*.
6. Anderson, J. M. The Biostratigraphy of the Permian and Triassic.
7. Haughton, S. H. Review of G. H. Findlay's book entitled "Dr. Robert Broom, F.R.S., Palaeontologist and Physician (1866—1951)".

Apart from these, papers by members of the staff, dealing with Institute material, have been published or presented during the year, as follows:

Dr. E. P. Plumstead

1. Two contributions to the *Standard Encyclopaedia of Southern Africa,* V(5).
   (a) Fossil Plants (2—11)
   (b) Gondwanaland (258—266)
2. The Late Palaeozoic Glossopteris Flora. In the *Atlas for Palaeobiogeography,* 167—215. Edited by A. Hallam and published by Elsevier Publishing Co., Amsterdam.

3. The Enigmatic Glossopteris Flora and Uniformitarianism, in V(1) (411—424) of *Implications of Continental Drift to the Earth Sciences* (Edited by D. H. Tarling and S. K. Runcorn, and issued by the Academic Press, London and New York).
4. Obituary Notice of the late Dr. B. B. Brock. *Yearbook of the Geol. Soc. London for 1972,* 30—31.

Dr. Plumstead also prepared for publication:

5. A new Assemblage of Plant Fossils from Milorgfjella in Droning Maud Land—Greater Antarctica—for the *British Antarctic Bulletin,* and
6. Trees of the Past, for the Institute of Forestry's Symposium on "Our Green Heritage", held in Pretoria in June, 1973.

B. R. Turner

1. A paper entitled "Statistical Appraisal of Triassic Molteno Sedimentary Cycles from the Upper Part of the Karroo System in South Africa" was submitted for publication in the *Journal of Sedimentary Petrology.*
2. Three other contributions are ready for submission to publishing bodies:
   (a) Some Aspects of the Stratigraphy and Sedimentary History of the Lower Beaufort beds in the Beaufort West district, with notes on Uranium mineralization.
   (b) Beaufort Stratigraphy: a Critical Appraisal.
   (c) Contribution to the Coal section of the *Mineral Resources Handbook of South Africa* (Geological Survey publication).

B. Maguire

1. The Ethno-botany of the Bushman (with H. J. Heinz). To appear as a special supplement to *Botswana Notes and Records.*
2. A brief summary of the !Ko food plants. To appear in the I.S.M.A. publication.

C. Gow

Habitual sheltering in an extensive cave system by baboons near Bredasdorp, Cape Province. *South African Journal of Science,* V(69), (1973), p. 182.

Professor P. V. Tobias

1. Paranthropus. In: *Standard Encyclopaedia of Southern Africa.* Cape Town: Nasou Ltd., V(8). 446.
2. Plesianthropus. In: *Standard Encyclopaedia of Southern Africa.* Cape Town: Nasou Ltd., V(8), 617.
3. Obituary: Dr. L. S. B. Leakey. *South African Journal of Science,* V(69) (3): 72—73.
4. Into the Pliocene. *South African Journal of Science,* V(69), 101.
5. The cultural and phylogenetic status of "Australopithecus Boisei" and of the australopithecines in general. In: *The Origin and Evolution of Man. Readings in Physical Anthropology.* (ed. Ashley Montagu), New York, Thomas Y. Crowell Company. 148—158.
6. Praeanthropus. In: *Standard Encyclopaedia of Southern Africa.* Cape Town: Nasou Ltd., V(9). 73.
7. Skildergat, C.P. In: *Standard Encyclopaedia of Southern Africa.* Cape Town: Nasou Ltd., V(9), 652.
8. Implications of the new age estimates of the early South African hominids. *Nature,* V(246), 79—83.
9. Louis Seymour Bazett Leakey 1903—1972 (and bibliography). *South African Archaeological Bulletin,* V(28), 3—12.
10. Editor of: Special Number of the *Journal of Human Evolution* in honour of Professor R. A. Dart, on the occasion of his 80th birthday. "Palaeoanthropological Progress, Problems and Perspectives", V(2), No. 6, 417—577.

VISITORS

The Institute has been honoured during the year by visits, of varying duration, of scientists from a number of countries outside the Republic who have come for study of the material that it houses and for discussion of problems which are of mutual concern.

Listed under countries they are as follows:

A. United States of America

1. Dr. Helen F. Goring, Hillsborough College, Tampa, Florida. Interested in the osteodontokeratic material.
2. Drs. R. Protsch and J. L. Bada, University of California. Dating of fossil bone from the Cave of Hearths and Border Cave.
3. Mr. Bryce Rensberger, of the New York Times. Science writer.
4. Dr. H. Barghusen, Medical School, University of Illinois, Chicago. Mastication in mammal-like reptiles.
5. Dr. D. Read, Department of Anthropology, University of California. Osteodontokeratic culture.
6. Dr. R. Bakker, Museum of Comparative Zoology, Harvard University. Vertebrate palaeoecology.
7. Drs. T. and P. Rich, The Museum, Texas Technical University, Lubbock, Texas. Fossil vertebrates.
8. Professor Wayne L. Fry, Museum of Palaeontology, University of California. Fossil Plants.
9. Dr. Max K. Hecht, Queen's College, City University of New York. Extinct Lizards.
10. Dr. B. Eisenhart, Harvard University. Fossil baboons.

B. France

1. Dr. C. Mendrez, Institut de Paléontologie, Muséum d'Histoire Naturelle, Paris. Karroo reptiles—Therocephalia.
2. Madame G. Petter, Institut de Paléontologie, Paris. Fossil carnivores from cave deposits.

C. England

Mr. J. Smart, Department of Zoology, Cambridge. Karroo reptiles.

D. Australia

1. Dr. A. A. Martin, Department of Zoology, University of Melbourne. Fossil mammals from cave deposits.
2. Dr. F. English (Optometrist), Brisbane. The pineal eye in early reptiles.
3. Dr. B. Riek, Division of Entomology, C.S.I.R.A., Canberra. Fossil insects.

E. Japan

1. Dr. K. Asama, National Science Museum, Tokyo. Palaeobotany.
2. Dr. J. Hasegawa, National Science Museum, Tokyo. Vertebrate fossils.
3. Dr. I. Fujiyame, National Science Museum, Tokyo. Fossil insects.
4. Dr. Y. Kanie, Yokosuka City Museum. Fossil invertebrates.
5. Dr. F. Takai, Geological Institute, University of Tokyo. Vertebrate fossils.

F. Madagascar

Father Otto Appert (Swiss missionary). *Glossopteris* flora.

G. Canada

Dr. R. Carroll, Redpath Museum, McGill University. Fossil reptiles.

In addition, Dr. A. Keyser of the Geological Survey in Pretoria was a frequent visitor to the Institute for study of specimens of Karroo anomodontia, a group in which he is specializing.

GENERAL

Our thanks are herewith expressed to the Vice-Chancellor and Council of the University for their generous support of the Institute and its work by the provision of the additions and alterations to the Douglas Smit House which have given the staff the opportunity to carry on their individual tasks in comfort and also for the unfailing help that has been given by the University staff as a whole. Thanks are also due, and offered, for the financial assistance given by the C.S.I.R.

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A BRIEF REVIEW OF THE FLORA OF THE MOLTENO "FORMATION" (TRIASSIC), SOUTH AFRICA

by
H. M. Anderson

ABSTRACT

A brief summary of the stratigraphy of the Molteno "formation" is given and the flora and fauna occurring at 42 known localities is reviewed. The flora is represented mainly by leaves (104 species) of which the seed ferns form the most dominant element, and by spores and pollens (53 species).

INTRODUCTION

Molteno plant fossils were first described by Feistmantel (1889). Du Toit while working for the Cape Geological Survey mapped large areas of Molteno outcrop and made plant collections from numerous localities. These collections were described by Seward (1903, 1908) and by Du Toit (1927). Both Thomas (1933) and Townrow (1959, 1962, 1967) made collections and described new material from the Upper Umkomaas locality. Fabre and Greber (1960) described a new species from the Morija locality. Since 1967 extensive fossil collections have been made from 38 new localities in the Molteno "formation". This has resulted in a substantial increase in our knowledge of the flora and fauna which is outlined in this paper; more comprehensive accounts are to be published in the future.

STRATIGRAPHY

The Molteno "formation" is the lowermost subdivision within the Stormberg "group" and is approximately of lowest upper Triassic age (? Carnian).

"Supergroups"	"Groups"	"Formations"
Karroo	Stormberg	Drakensberg Lava
		Cave Sandstone
		Red Beds
		Molteno
	Beaufort	
	Ecca	
	Dwyka	

(N.B. The status and nomenclature of the various subdivisions within the Karroo Basin are being revised by a national committee. The old terminology is used here.)

A regional study of the formation is at present being completed by Turner who has compiled a detailed outcrop map from which Fig. 1 has been drawn. The following statements have largely been extracted from his work. The Molteno "formation" exhibits a cyclic pattern of sedimentation. Seven cycles are recognised along the southern outcrop belt, where the formation attains its fullest development. The cyclic sedimentation is thought to be a reflection of the recurrent uplift and denudation of the major source area to the south-east (i.e. the Cape fold mountains). Only the second cycle is basin wide in extent and was probably the result of the strongest upthrust of the source area. The majority of the good plant localities occur in this second cycle (see Table 1). Turner (1970) recognised in the ideal cycle a sequence of four major facies as follows:

(a) ". . . . conglomerate overlying an erosional surface (which appears to be the result of erosion and deposition within a braided river channel wandering across a flood plain";
(b) Variously bedded coarse to fine sandstones which show ". . . all the characteristics of a modern point bar complex";
(c) Siltstones and silty shales " . . . deposited mainly from suspension in the quiet parts of the channel or in abandoned channels during low water";
(d) Shale and coal probably representing ". . . overbank deposits from flood waters in the quiet back swamp areas of the flood plain".

It is in facies (d) that the best deposits of fossil plants occur.

The physiographic conditions which prevailed during Molteno times are summarized in Fig. 1. The highland areas are adapted from Ryan (1967) and Anderson and Anderson (1970); the palaeolatitude from Robinson (1971, Fig. 5), and the current directions from Turner (1974, personal communication).

The Molteno "formation" was probably deposited on a large fluviatile plain with most of the sediment being derived from the south and south-east. The rivers transporting the sediment were predominantly braided in character closer to the source area where the gradient was correspondingly steeper; however, where the rivers devolved into the flood-plain proper and where the slope levelled-off the rivers became more meandering in character.

Fig. 1 (a). PALAEOGEOGRAPHY DURING DEPOSITION OF THE MOLTENO 'FORMATION'

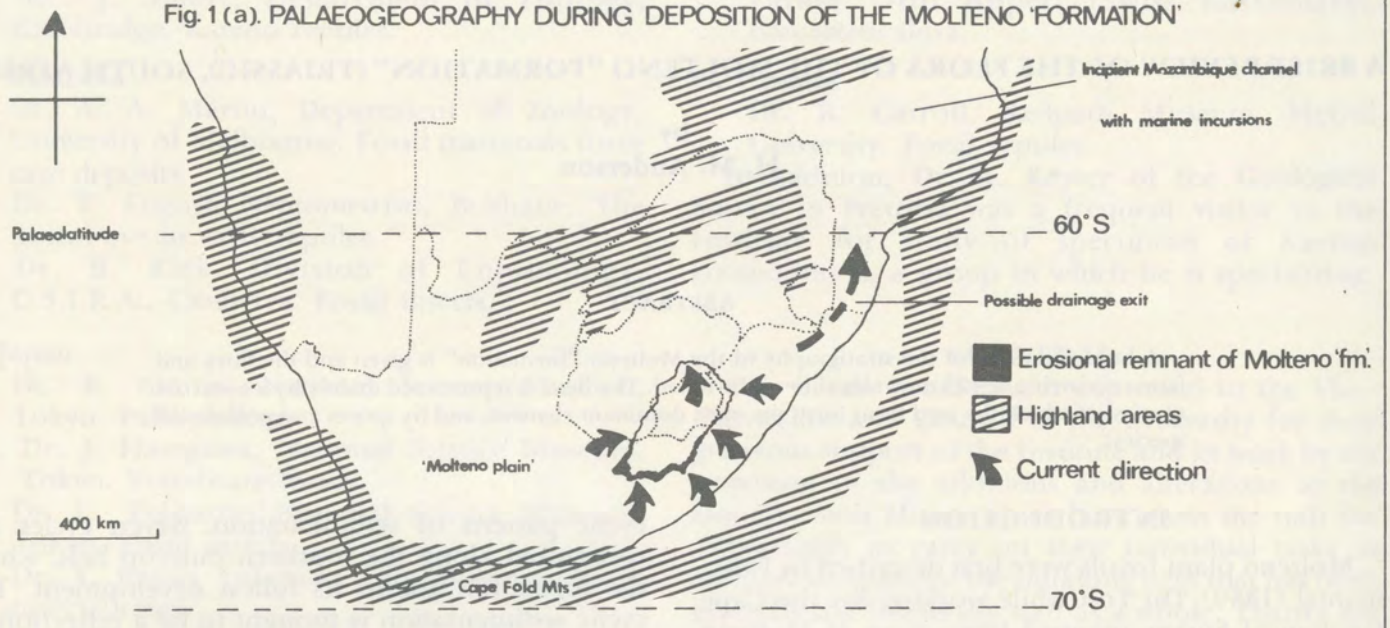

Fig. 1 (b). MOLTENO FORMATION OUTCROP AND PLANT LOCALITIES

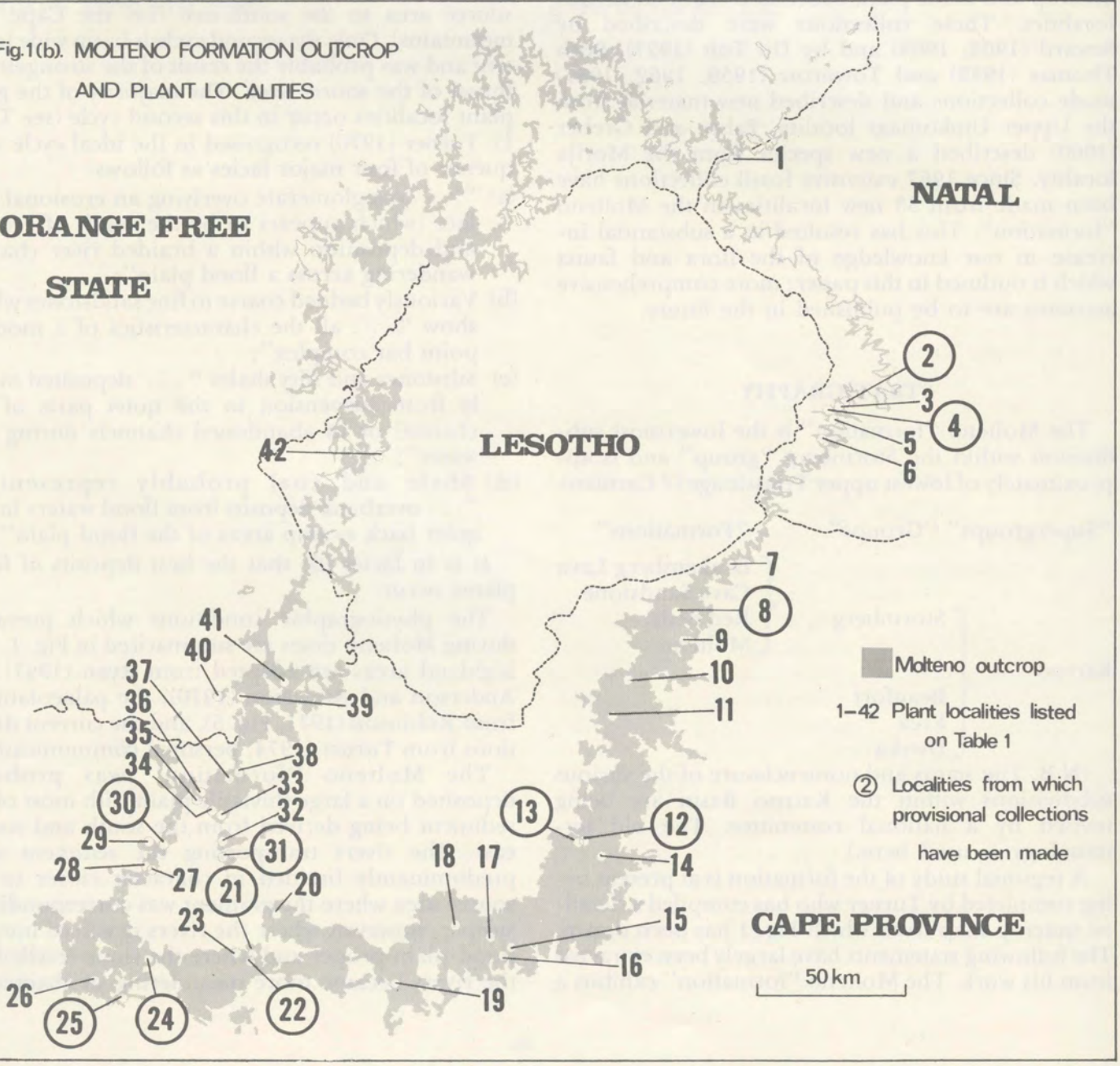

Table 1
Molteno Macroflora—locality data

Number on Fig. 1	Province or Country	Locality	- Code	Molteno 'fm' cycle number	Number of 'leaf' species	Number of catalogued blocks	General quality of material	Nature of collection made to date		
								provisional	fair to good	comprehensive
1	Natal	Little Switzerland	N—L.Sw.	2	42	1 130	good			√
2		Hlatimba I	N—Hl.I	2	2	15	fair		√	
3		Hlatimba II	N—Hl.II	2	?	73	good	√		
4		Upper Umkomaas II	N—U.U. II	2	?	14	good	√		
5		Upper Umkomaas	N—U.U.	2	50	1 213	good			√
6		Sani Pass	N—S.P.	2	20	276	good			√
7	Cape	Afsondering	C—Af.	2	8	67	fair		√	
8		Matatiele II	C—Mt. II	±2	?	31	poor	√		
9		Matatiele I	C—Mt. I	2	19	364	good		√	
10		Kenegapoort	C—Kp.	3b	3	32	fair		√	
11		Mount Fletcher	C—M.F.	3b	?	90	fair		√	
12		Maclear I	C—Mc. I	3b/4	4	67	good		√	
13		Maclear II	C—Mc II	6	?	17	fair	√		
14		Maclear III	C—Mc III	6	?	10	fair	√		
15		Rooipoort	C—Rp. I	2	36	300	good			√
16		Konings kroon	C—K.K. I	2	34	250	good			√
17		Lagg	C—Lg.	±4	14	84	fair		√	
18		Elliot	C—E. I	±4	4	70	fair		√	
19		Askeaton	C—As. I	1	9	160	fair		√	
20		Dordrecht I	C—Dt. I	4/5	3	24	poor		√	
21		Dordrecht III	C—Dt. III	±5	?	41+	fair	√		
22		Dordrecht IV	C—Dt. IV	±5	?	35	fair	√		
23		Dordrecht II	C—Dt. II	±5	26	1 096	fair			√
24		Boesmanshoek Pass	C—B.P.	4/5	?	12	poor	√		
25		Bamboesberg	C—Bb.	1	?	16	fair	√		
26		Molteno I	C—Mo. I	1/2	9	55	fair		√	
27		Klein Hoek	C—K.H.	2	13	158	fair		√	
28		Klein Hoek II	C—K.H. II	2	1	13	fair		√	
29		Kullfontein	C—Kf.	?	3	10	poor		√	
30		Kommandokop	C—Kd.	±3a	?	10	fair	√		
31		Jamestown	C—Jt.	±4	?	12	poor	√		
32		Telemaghus Spruit	C—T.S.	3a/4	11	134	fair		√	
33		Vineyard II	C—Vy. II	2	2	44	poor		√	
34		Vineyard I	C—Vy. I	3a	9	163	fair		√	
35		Vineyard III	C—Vy. III	3a	9	231	fair		√	
36		Vineyard IV	C—Vy. IV	2	4	63	fair		√	
37		Plaatkop	C—Pk.	3a	1	24	fair		√	
38		Kraai River	C—K.R.	3a	7	183	fair		√	
39	O.F.S.	Rouxville I	O—R. I	2	10	144	fair		√	
40		Rouxville II	O—R. II	2	7	127	fair		√	
41		Zastron	O—Za. I	2	13	66	fair		√	
42	Lesotho	Morija	L—M	2	3	37	fair		√	

A drainage exit may have existed in the north-east leading into the incipient Mozambique Channel. When the flood plain and source area achieved a state of near equilibrium and very little or no drainage existed conditions would have been ripe for the development of swamps dotted about the landscape.

LOCALITY AND COLLECTING DATA

A special effort has been made to assemble comprehensive collections of fossil plants from as many good localities as possible. From a few of these localities rare faunal elements have also come to light.

The 42 localities from which collections have been made are indicated in Fig. 1b and other relevant information thereon is summarised in Table 1. These form a good scatter throughout the outcrop, being more common towards the south where the formation attains its greatest thickness and extent. The position of each locality within the succession of cycles is given in Table 1 (personal communication, Turner, 1974).

The comprehensiveness of the collection made at each locality depends primarily on the quality of the material. Thus the most extensive collections (amounting to over 1 000 specimens each) have been made from Little Switzerland (1), Upper Umkomaas (5) and Dordrecht II (23), which yield excellently preserved fossils. The collections now total 6 961 catalogued specimens of selected material and are housed at the Bernard Price Institute for Palaeontological Research.

Of some 21 localities recorded from the Molteno "formation" by Du Toit (1927) only four have been relocated. Of these the most important is Upper Umkomaas (5) also known as "The Waterfall" or "Burnera" from which both Thomas (1933) and Townrow (1959) have also made collections and described material. Du Toit's other localities are very difficult (or impossible) to relocate, as insufficient data are available regarding their exact whereabouts. His collection which is housed in the South African Museum, Cape Town, forms the only other substantial collection outside of the Bernard Price Institute.

FAUNA

Faunal remains are extremely rare in the Molteno "formation" and to date are known only from localities where the dominant components are plants, i.e. 9 of the 42 localities herein mentioned. They consist of:

Crustacea	—	1 species (100 specimens from 1 locality)
Insects	—	32 species (84 specimens from 9 localities)
Fish	—	1 species (3 specimens from 1 locality)

Except for the 5 insect remains found by Townrow in 1956 and described by Zeuner (1961) these have all been found during the present collecting programme. The majority of specimens came from Dordrecht II (23) which is partly a reflection of intensity of collecting. The insect remains found prior to April 1972 have been described by Riek (1974).

Although earlier works have suggested that certain tetrapod vertebrate specimens have been found within the formation, both Turner (1972) and Kitching (1974, personal communication) indicate that this is not so. The three fish impressions found at Dordrecht II (23) and described as *Semionotus capensis* by Jubb (1973) thus represent the only known vertebrate material to date.

FLORA

Within the Molteno "formation" an abundant diverse flora is preserved which was first reviewed by Du Toit (1927). Subsequent workers and the present study have added to our knowledge, creating the need for another revision. For example, within the leaf fossils alone, there are at least 33 new species awaiting description. A concise summary of the floral composition is given in Tables 2 and 3, which are discussed below, while Table 4 provides an analysis of species frequency. Finally a brief impression of the vegetation during Molteno times is given.

Molteno flora—generic list (Table 2)

This tabulates in three separate columns the genera of leaves, fertile structures, and spores, pollen grains and acritarchs thus far recognised and indicates, as far as possible, the associations between these groups of organs. The relative or absolute abundance of each genus, and the number of species recognised in each, is given.

The leaves, fruits, seeds and sphenophyte stems have been studied by myself while J. M. Anderson has studied the spores, pollen grains and acritarchs. Silicified wood and other stem remains are not reviewed here.

The number of genera and species thus far recognised are:

Leaves	32 genera, 104 species
Fertile structures (fruits, seeds, etc.)	31 genera, 42 species
Spores, pollen grains and acritarchs	30 genera, 53 species

The 31 genera of "fertile structures" do not represent the equivalent number of plant genera. Different organs of the same parent genus (e.g. male and female cones, cones and seeds) are afforded different titles. The "fertile structures" found to date probably represent only about half of the 32 leaf genera known.

Of the 30 microfloral genera, 8 are acritarchs (unicellular organisms of unknown affinities). These

Table 2

MOLTENO FLORA—GENERIC LIST (excluding silicified wood)

Division	Leaves: Genus	spp.	Relative abundance	Fertile structures: Genus	spp.	Relative abundance	Spores and pollen grains: Genus	spp.	Relative abundance
Incertae sedis (non vascular plants)							8 genera	± 13	
Bryophyta	Hepaticites	1	rare						
	Muscites	1	rare						
Lycophyta							Aratrisporites	2	rare
Sphenophyta	Neocalamites	4	abundant	Strobilites	2	very rare			
	Phyllotheca	2	uncommon				Uvaesporites	± 2	uncommon
	Paraschizoneura	1	common				Osmundacadites	3	uncommon
	Incertae sedis (2)	2	very rare				Lophotriletes etc.	3	uncommon
Filicophyta	?Asterotheca	1	common		1		Dictyophyllidites	1	rare
	Todites	2	uncommon	fertile fronds	2	very rare	Duplexisporites	1	rare
	Dictyophyllum	1	very rare		1		Annulispora	2	rare
							Apiculatisporis	2	very rare
Pteridophylla	Cladophlebis	2	very rare				Endospora	1	very rare
	Pecopteris	1	very rare				Punctatosporites	2	rare
	Asplenites	3	very rare				Polypodiisporites	1	rare
	Kurtziana	1	very rare				± 4 genera (alete forms belonging either to spores or pollen grains)	± 8	uncommon
	Thinnfeldia	2	rare						
	Chiropteris	10	rare						
	Incertae sedis (3)	3	rare						
Glossopteridophyta	Glossopteris	2	uncommon						
Pteridospermophyta	New genus	2	uncommon						
	Dicroidium	21	abundant	Umkomaasia ♀	± 4		1 genus (non-striated disaccates)	6	abundant
				seeds	± 2	uncommon			
				Pteruchus ♂	± 4				
	Lepidopteris	1	common	Peltaspermum ♀	1	uncommon			
				Antevsia ♂	1		Cycadopites	1	abundant
Incertae sedis	Yabaeiella	3	uncommon	Fraxinopsis ♀	1	uncommon			
	Taeniopteris	4	common						
Cycadophyta	Pseudoctenis	18	uncommon						
	Nilssoniopteris	2	rare				Praecolpatites	1	very rare
Ginkgophyta	Ginkgo	1	rare						
	Ginkgoites	5	uncommon				2 gen. nov.	2	rare—very rare
	Baiera	4	common	inflorescence ♀	1	uncommon			
				Stachyopitys ♂	2				
Incertae sedis	Phoenicopsis	1	abundant	scales ♀	1	common			
				cones ♂	1	rare			
Coniferophyta	Rissikia	3	uncommon	seed cone ♀	1	very rare	Protohaploxypinus	1	rare
				pollen cone ♂	1				
Incertae sedis				5 seed genera	5	uncommon			
				11 cones/fruit genera	11	very rare	Hamiapollenites	1	very rare

Notes:
(1) Divisions according to Boureau 1970.
(2) Generic list of spores and pollen grains—Anderson (J. M.) pers. comm. 1973.
(3) Present estimate of total number of species known in Molteno Fm. is 104 leaf species + lycophyle spore species i.e. 106 (in 33 genera).

8 genera (2 of which are possibly the spores of the Bryophyta *Hepaticites* and *Muscites*) cannot be included in an estimation of the total number of genera and species of plants occurring in the Molteno "formation". One genus *Aratrisporites* (with 2 species of spore) is known definitely to belong to the Lycophyta which are unrepresented in the Molteno macroflora. These 2 species of lycopods can be added to the macrofloral list to raise the total known flora to 33 genera and 106 species.

The information on stem remains (other than sphenophyte stems) is too scanty at present to add anything to the overall floral list. Silicified wood, however, occurs sporadically throughout the Molteno "formation" and is found at or near localities 1, 11, 17, 20, 23, 32, of this paper.

Table 3.

MOLTENO MACROFLORA (four genera and species occurring at 31 localities)

Notes:

On this chart are included the 31 localities (of the 42 total) from which were made fair, good or comprehensive collections.

Where the relative percentage is given for each species the figure is based on counts or estimates made at the locality. Where the number of specimens is given the figure is based on the number of catalogued specimens available.

In order to give a comprehensive species list for the Molteno, 4 species which do not occur at any of the 31 localities are here listed:
Chiropteris zeilleri Seward 1903 [from Cyphergat (Du Toit?)]
Pseudoctenis sp. H and J. [Du Toit 1927 from Maclear (Du Toit)]
Pseudoctenis sp. K [this paper from Hlatimba II (N-H. II)]

Key:

4 — The different species bracketed by the unbroken line are considered to form part of a single variable species at the particular locality in question.

4 - - - The broken line purely connects members of a variable species which are separated on this chart. The % figure is placed according to the dominant component.

(1) Encircled numeral indicates number of catalogued specimens in collection.

1 Simple numeral indicates relative percentage.

✓ Indicates less than one percent.

Locality	code	Plant horizon named according to dominant element(s) + placed in stratigraphic order.	Bryophyta	Sphenophyta	Filicophyta	Pteridosperm. (new genus)	Pteridosperm. Dicroidium	Pteridosperm. Lepidopteris	Insertae sedis Sagenopteris	Insertae sedis Taeniopteris	Cycadophyta	Sinkgo + Ginkgoites	Baiera	Phoenicopsis	Insertae sedis Coniferophyta
Little Switzerland	N-L.Sw		✓	✓	✓	✓	17	73	✓		1	1	✓	2	3 1
Hlatimba I	N-Hl. I			99				✓							
Upper Umkomaas	N-U.U.		✓	3	✓	✓	2	78	2		2	3	✓	2	5 3
Sani Pass	N-S.P.		✓	✓		✓		90	7	1	2	✓	✓		5
Afsondering	C-Af.							93			2		✓	✓	5 ✓
Matatiele I	C-Mt. I			✓		1		90	2		2	✓	✓	✓	5
Kenegapoort	C-Kp.				✓			99							
Mount Fletcher	C-M.F.			100		✓									
Maclear I	C-Mc. I							99			1		✓	✓	
Rooipoort	C-Rp. I C	Dicroidium				1		84	✓	2	✓	10	✓	2	✓
	C-Rp. I A,D	Ferns + Cycads		20	50	✓	5				✓	25			
	C-Rp. I B	Phoenicopsis						5							95
Konings Kroon	C-K.K. I A C-S	Dicroidium			✓	✓		75	2	✓	1	5	7	✓	7 2
	C-K.K. I →	Neocalamites		90											10
	C-K.K. I B	Phoenicopsis		20		2		5							70
Lagg	C-Lg. A	Phoenicopsis		10	20	✓					✓				70
	C-Lg. B	Ferns		10	80	✓									10
Elliot	C-E. I	Neocalamites		100											
		Dicroidium						100			✓				
Askeaton	C-As. I	Neocalamites		100											
		Dicroidium		5	40			20	30				5		
Dordrecht I	C-Dt. I				20						20			60	
Dordrecht II	C-Dt. II			✓	1	✓	✓	3	3	✓	✓	✓	✓	82	10
Molteno	C-Mo. I			✓	✓	20	2	✓			✓				78
Klein Hoek	C-K.H.	Neocalamites		99											
		Phoenicopsis		10											90
		Dicroidium				✓		45	4		10			✓	40 1
Klein Hoek II	C-K.H.II													100	
Kulfontein	C-K.f.								✓		✓			99	
Telemaghus Spruit	C-T.S.			✓	✓	✓		23	1		2		✓		75
Vineyard II	C-Vy. II			100											
Vineyard I	C-Vy. I		✓		✓	✓		70			4	✓	1	✓	25
Vineyard III	C-Vy. III				✓			87	✓	✓	4	✓	2	1	5
Vineyard IV	C-Vy. IV	Neocalamites		80	20										
		Phoenicopsis + Neocal.		40											60
		Dicroidium + Phoen.						60							60
Plaat Kop	C-Pk.			100											
Kraai River	C-K.R.				✓	✓		95	✓		4			✓	
Rouxville I	O-R.I.			✓	✓	✓		70			✓			30	✓
Rouxville II	O-R.II	Phoenicopsis													100
		Neocalamites		100											
		Dicroidium						99				✓	✓	1	
Zastron	O-Za. I			✓	✓	✓	✓	10	10					80	
Moriia	L-M.								99		✓				

Species frequency categories (see text and table 5) →	4B	3B	1C	1B	1B	4D	2D	2D	1C	1+4D	1+4D	1B	1B	2D	4D	4C	4D	3D	4C	3D	4C	3C	2D	4D	3/4D	3C	3C	4B	3C	2C

BRYOPHYTA

	Equisetites	Tourneya 1889
	guesselini	Tourneya 1889
	A (new species)	Neocalamites
	carrerei	(Zeiller 1903) Hale 1908
	(+bladed stems)	
	B (new species)	
	A (new species)	
	cf. equisetiformis	Schaumburg 1979
	A (new species)	
	(stems)	
	A (new species)	
	A (new species)	
	B (new species)	
	A (new species)	
	A (new species)	
	A (new species)	
	A (new species)	
	cf. marrensis	Brongniart 1828
	A (new species)	
	A (new species)	
	B (new species)	
	C (new species)	
	cacheutensis	(Kurtz 1921) Frenguelli 1942
	capensis	(Frenguelli 1947) comb. nov.
	praecordillerae	Frenguelli 1944
	elliotensis	Anderson & Anderson 1985
	Incertae sedis	
	Cuneata	Carruthers 1869
	Blade	Bell 1956
	A (new species)	
	Walta kliersis	Bell 1956
	B (new species)	

SPHENOPHYTA

	Phyllotheca	Schaumburg 1979
	Paracalamites	
	Incertae sedis	

FILICOPHYTA

	Asterotheca	(Kurtz 1921) Frenguelli 1942
	Taeniopteris	
	Dictyophyllum	Kurtz 1921
	Cladophlebis	
	Pecopteris	
	(New genus)	

PTERIDOSPHYLLA

	Incertae sedis	
	Chiropteris	

The Molteno Macroflora (leaf genera and species occurring at 31 localities) (Table 3)

The 31 localities (of the 42 total) listed are those at which fair to comprehensive collections have been made. At certain of these localities more than one fossiliferous horizon occurs, each carrying a different macrofloral assemblage. These are included separately on Table 3 and referred to as:

"Graded horizons—at six localities, two or three "graded horizons" can be recognised in which very different macrofloral assemblages occur. These horizons and assemblages, however, grade into one another with little or no barren strata separating them.

"Distinct horizons"—at two localities, "distinct horizons" can be recognised in which very different macrofloral assemblages occur, separated by barren strata greater than one metre in thickness.

A comprehensive list of the leaf genera (including Sphenophyte stems) is set out in taxonomic order according to the major groups proposed by Boureau (1970). For each locality the species occurring are recorded either as a relative percentage or the total flora or as an actual number of catalogued specimens (in cases where the relative percentage is less than one).

In the case of the genera *Dicroidium* and *Lepidopteris* solid and dotted lines are included on the table for the following purpose. At any particular locality a species exhibits a distinct range of morphological characters. This range does not always compare with that of a described species and frequently overlaps with that of one or more similar species. A solid line links such species whilst dotted lines are incorporated when the species concerned do not adjoin each other on the table. The *Dicroidium* species (with the provisional names given in brackets) correspond to those used in the key on chart 9 of Anderson and Anderson (1970).

Table 4
Species Frequency Categories

Number of localities at which particular species occurs → / Frequency per locality of particular species ↓	**A** At a high proportion of localities at > 25% of } localities at > 8	**B** At several localities at 7—25% { localities at 5—8	**C** At a few localities at 2—4 localities	**D** At one locality
1 *Common-abundant* Where a population is easily collected and a selection of the best material can be made.	**1A** (5)	**1B** (8)	**1C** (18)	**1D** (5)
2 *Uncommon* Where after many man hours collecting every fair to good specimen must be kept to form a population. > 10 fair-good specimens.	**2A** (—)	**2B** (5)	**2C** (5)	**2D** (10)
3 *Rare* Where after many man hours of collecting only a few specimens have been found. 3—10 specimens.	**3A** (—)	**3B** (1)	**3C** (11)	**3D** (8)
4 *Very-rare* Where after many man hours of collecting only 1 or 2 specimens have been found. 1—2 specimens.	**4A** (—)	**4B** (2)	**4C** (8)	**4D** (14)

Notes: At the 31(+4) 'localities' (+ 'distinct horizons') listed on chart 3, 100 species occur which are allocated to species categories. The number of species falling in each category is here given (encircled figures above).

"Species frequency" categories (Table 4)

An analysis of the flora into "species frequency" categories is presented. The categories indicate the relative frequency of occurrence of the species found in the Molteno "formation" and are based on the combined consideration of number of localities and abundance per locality. Each of the two variables is split into four categories giving a total of sixteen. For simplicity they are referred to by the relevant number (1 to 4) and letter (A to D) e.g. 1A, 2A, etc.

At the bottom of Table 3 each species has been given an appropriate category rating. In most cases a particular species is easily placed in one or other category. Difficult cases do, however, arise e.g. *Baiera schencki* which occurs at ten localities, but only commonly at five and has been placed in category 1B rather than 1A. The encircled figures on Table 4 indicate the number of species falling into each category. Thus it can be seen that five different species fall in category 1A, eight into 1B, none in 2A etc.

This gives an overall picture of our knowledge of the Molteno flora and could be a useful method of providing essential information with floral lists.

For example *Neocalamites carrerei* 1B, immediately indicates that this is a common to abundant species found at some five to eight localities. The usage of these "species frequency" categories could greatly increase the reliability of comparisons between floras and would thus also improve interregional correlations.

DISCUSSION

The general impression of the Molteno vegetation that can be envisaged at present is:

(a) An extensive well-watered plain (1 500 km by 750 km), populated by at least 33 genera and 106 species of macro plants.

(b) The 106 species included trees (e.g. conifers and ginkgos), woody shrubs (e.g. cycads and larger forms of *Dicroidium*), ground cover (e.g. ferns and possibly the smaller forms of *Dicroidium*) and swamp growth (e.g. sphenophytes and possibly *Phoenicopsis*).

(c) In general the pattern of vegetation throughout the plain was probably fairly uniform, but local variation certainly occurred in different specialised habitats.

(d) The most diversified and abundantly preserved plant group was the genus *Dicroidium*. At certain localities (or "distinct" or "graded horizons") certain genera (e.g. *Neocalamites, Phoenicopsis* or *Baiera*) occur more or less to the exclusion of other plants. At Klein Hoek (28), for instance, three "graded horizons" occur with distinctly different plant associations:

"upper horizon" —*Neocalamites* predominant (99%)

"middle horizon" —*Phoenicopsis* predominant (90%)

"lower horizon" —*Dicroidium* (45%), associated with several other genera.

This is possibly an indication of a changing environment from lake to swamp.

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I would like to thank Dr. E. Plumstead, Dr. J. Kitching, Dr. A. Cruickshank and the University of the Witwatersrand for the many ways they have helped in this project. To Brian Turner I am very grateful for finding most of the localities and for permission to use the outcrop map of the Molteno "formation". Particular thanks go to my family and the many friends and farmers who have offered generous hospitality and aid whilst collecting the fossils. I am grateful to Natal Parks Board, Department of Forestry and the Monuments Commission for issuing the necessary collecting permits and to African Explosives for blasting. To Dr. J. Townrow special thanks for the collection (of 369 catalogued blocks) from Upper Umkomaas. There is one person I will never be able to thank sufficiently and that is my husband John, who has been my closest companion and greatest help throughout this project.

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SEED-BEARING GLOSSOPTERIS LEAVES

by

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Seeds are commonly known elements of *Glossopteris* floras. The connection of these seeds to any definite elements in the floras and their systematic position with it has always been uncertain, and they are usually referred to as a group "incertae sedis". Several of these seeds have been described and placed in the genera *Cardiocarpus* Brongniart, *Cordiocarpus* Geinitz and *Samaropsis* Goeppert, specially erected for them. Arber (1905, p. 206) noticed the common occurrence of seeds with *Glossopteris* leaves, and refers to them without any further conclusion as "A few seeds . . . in association with fronds of *Glossopteris browniana*. The seeds are possibly referable to *Cardiocarpus*".

In 1973, two *Glossopteris* leaves were found at Hammanskraal, some 50 km north of Pretoria, at separate times, evidently in the same stratum where the seed hitherto classified as *Cardiocarpus* occurred. On each a seed was in organic connection with the midrib of the leaf. Both specimens here described belong to the same species, as can be ascertained from all morphologic characters of both the seeds and leaves. The generic characters of *Glossopteris,* as defined by Brongniart (1828, original description 1822) from the leaves, are clear: "Fronde simple entière, plus ou moins lancéolée, rétrécie insensiblement vers sa base; nervure moyenne large à sa base, s'évanouissant vers le sommet, et donnant naissance à des nervures secondaires, fines, arquèes. oblique, dichotomes, quelqefois anastomosées à leur base".

The plant fossils are found in an abandoned quarry in carbonaceous shales of the Middle Ecca Stage in the north-western corner of the farm Haakdoornfontein 119 JR, 7,25 km almost due south of Hammanskraal. The locality is situated at latitude 25° 28′ 15″ and longitude 28° 17′ 40″.

The quarry was worked for fire clay and is situated about 150 m east of the new highway between Pretoria and Warmbaths.

The seed-bearing *Glossopteris* leaves clarify the systematic position of the seed-genus *Cardiocarpus* Bgt. (1828) the latter being the seed of the earlier described *Glossopteris*. Thus *Cardiocarpus* has to be considered as a junior synonym of the genus *Glossopteris* Bgt.

On the second specimen, hereunder referred to as specimen "B" (catalogue No. H I 99), the seed sits on the midrib in a seminatural position, but is pressed flat on the surface of the leaf without any breakage or dislocation. On this specimen the external characters of a connected seed can be studied complete with the megasporophyll. On the first found specimen, "A" (catalogue No. H 1 74), the seed is partly broken off and a part of the megasporophyll is missing, exposing the connections between the inner tissues of the seed and those of the midrib. The comparative study of these two specimens provides clear evidence on the type of reproduction of *Glossopteridae* and refers the group to *Pteridospermophyta*.

The seed sits on the midrib without a stalk and is directly connected to it through the megasporophyll. The structure of both seeds is very similar. Specimen "A" (Figures 1—4) shows that sarcotesta is pointed oval (17 mm × 11,5 mm), with deep emargination at its apex. Its soft consistency is indicated by the transparent midrib at the apical part of the right margin (Figures 2 and 3). The sclerotesta is also pointed oval (11 mm x 6,5 mm) and was apparently much harder than the sarcotesta, possibly more or less stony, indicated by the interruption of the transparent midrib at its margin. A part of the megasporophyll is preserved at the right side of the base of the seed and its imprint is marked on the whole breadth of the base. The left half of the megasporophyll was removed during preparation, exposing a bundle of veins connecting the base of the sarcotesta with the inner tissues of the midrib of the leaf. The bundle of connecting tissue is about 1 mm below the surface of the midrib, possibly due to fossilisation pressure. It is in the shade of the cavity in figure 3, but is clearly visible in the more vertically illuminated figure 4. On the horizontally illuminated figure 3 the imprinted surface structure of the seed can be better examined. The present position of the seed is a result of the process of fossilisation. The sitting seed apparently broke off under pressure as it has no flexible stalk and remained connected to the midrib through the more elastic tissues of the soft sarcotesta.

Morphology of the seed Specimen "B" (Figures 5 and 6) is similar. Sarcotesta 15 mm long and 11 mm broad, sclerotesta 10 mm long and 7,5 mm broad. The megasporophyll is complete on this specimen exposing its near-lateral side joining the midrib of the leaf within the margin of the latter. Its apical portion supports the sclerotesta. The sarcotesta joins the megasporophyll at its sides and most likely embraced it when alive.

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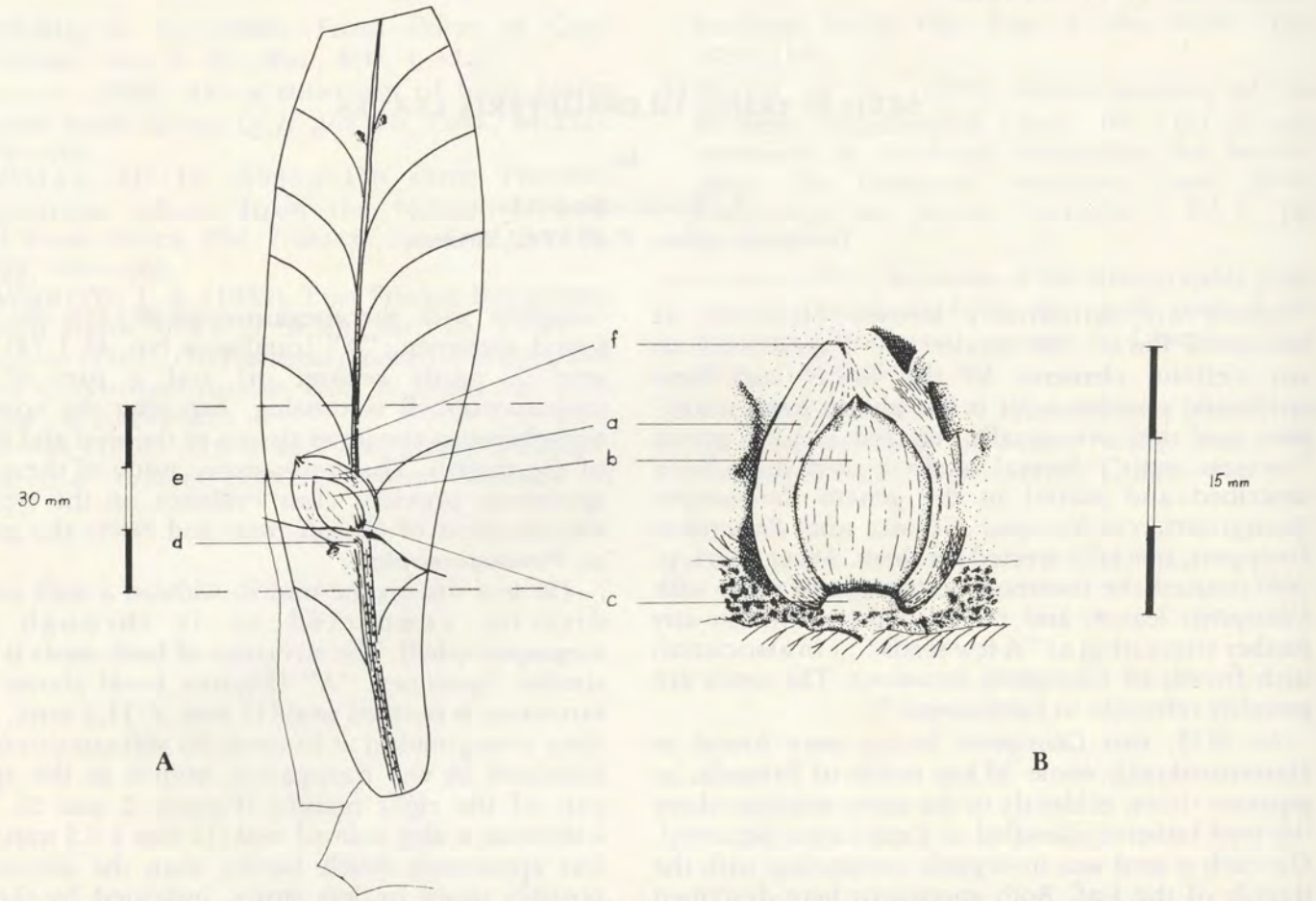

Fig. 1 Morphological terms of *Glossopteris* seeds. A= specimen "A", cat.no. H I 74; B = specimen "B", cat.no. H I 99. a = sarcotesta; b = sclerotesta; c = megasporophyll; d = connecting tissues of sarcotesta of specimen A; e = midrib of leaf transparent through the sarcotesta on specimen A; f = micropyle. The curved lines on the surface of leaf (A) indicate the trend of dense secondary venation. The broken horizontal lines on (A) demarcate the section shown on figures 2 and 3.

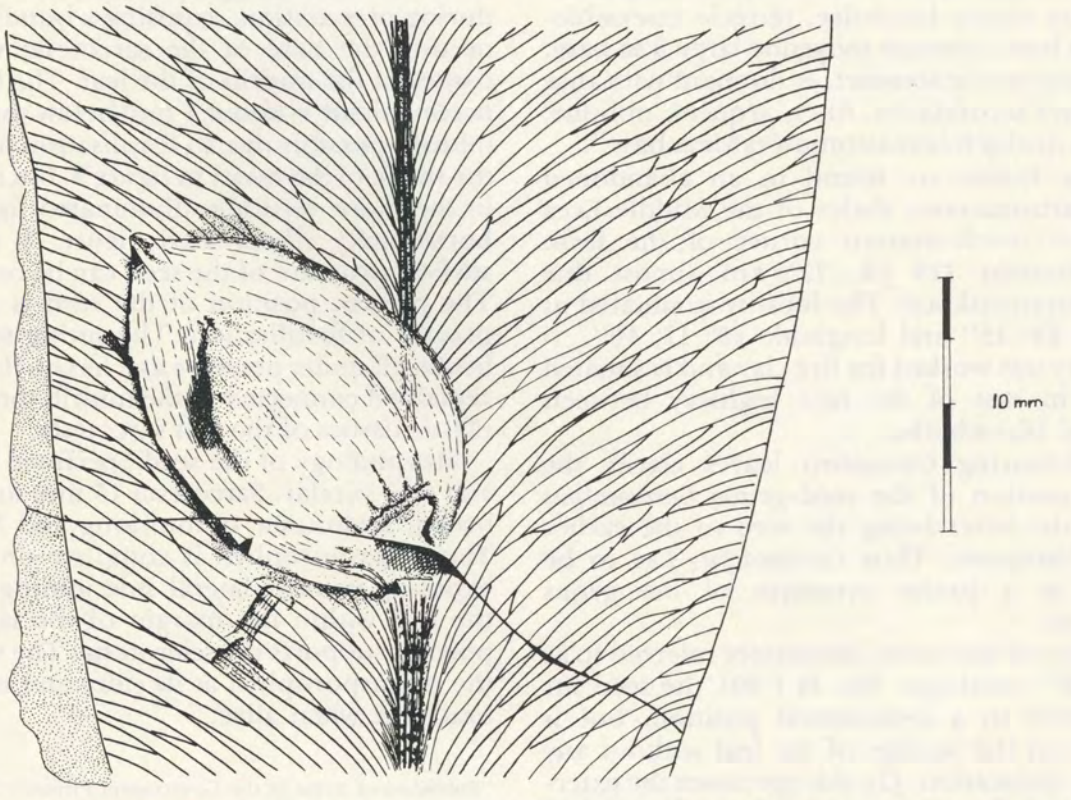

Fig. 2 *Glossopteris* seed (sepcimen "A", cat.no. H I 74). Enlarged part of leaf as marked on figure 1.

The leaf. The leaves of the *Glossopteridae* are not completely analogous with the leaves of *Gymnospermae* and *Angiospermae*. By definition a leaf of these groups is vegetative, and never bears reproductive organs. What we call a "leaf" in *Glossopteridae* has the combined function of assimilating and bearing reproductive organs.

The apices of the leaves are missing on both specimens, a greater part being preserved on specimen "A", but more of the base is visible on specimen "B". On specimen "A" the margins of the preserved portion of the leaf are already curved towards the apex and contracted towards the base, consequently it can be assumed that the complete leaf could not have been much longer. The preserved portion is 130 mm long, with a maximum width of 33 mm. The shape is oblanceolate, broadest above the middle, tapering towards the base and more rapidly towards the apex.

On specimen "B" the midrib is fairly broad, 4 mm under the seed, 3 mm above it. The petiole is 14 mm long, with maximum width 12 mm at the base.

The leaf is slightly asymmetric. The midrib is distinct, extending through the surface, broader at the base and gradually narrowing above the seed towards the apex. The surface of the midrib is longitudinally striated, with rows of fine tubercles in specimen "A", but appears as an amorphous surface in specimen "B". This rough surface is definitely not the imprint of the cuticle, which is missing, but of an inner tissue. Similar rough midrib surface was found in several species of *Glossopteris* and bears no taxonomic significance.

Secondary venation is fine. The meshes are very regular in shape and size through the whole leaf, being shorter and narrower only near the margin. The veins leave the midrib at an acute angle and then curve to the margin. The density of the veins is about 20—26 per cm.

Glossopterid fructifications have been identified and described by Plumstead and by other investigators on several occasions. In view of the present evidence it would appear that these should be interpreted as male organs. Both they and the organs now described and considered to be female organs are attached to the midrib of the leaf.

The specimens described are preserved in the Collection of the Geological Survey, Pretoria, under the catalogue numbers H I 74 and H I 99.

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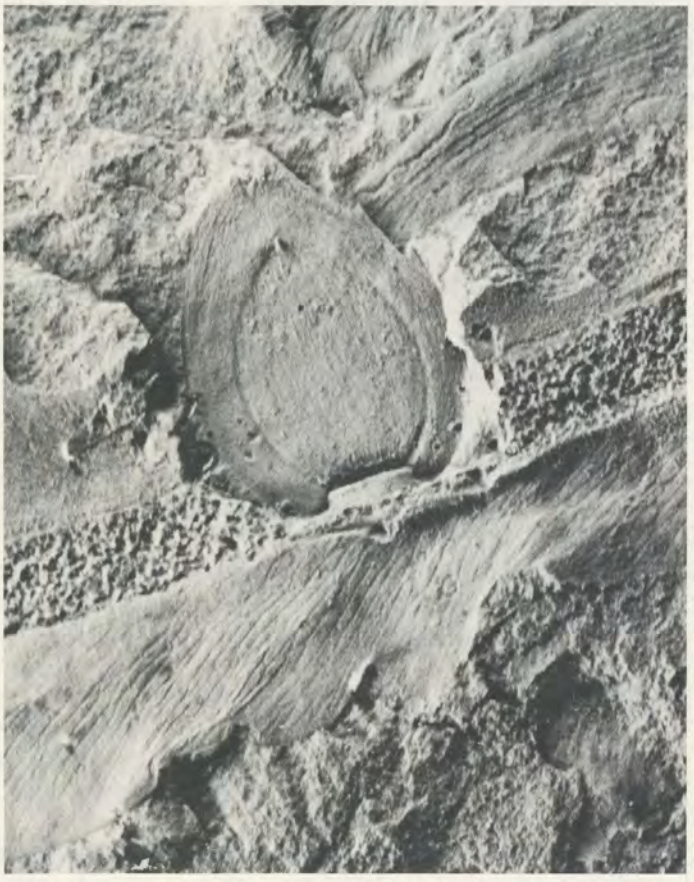



Fig. 3 A section of the seed-bearing *Glossopteris* leaf as marked on figure 1. (specimen "A", cat.no. H I 74).
Fig. 4 Enlarged picture of the *Glossopteris* seed in semivertical illumination showing the connecting tissues of sarcotesta to midrib (specimen "A", cat.no. H I 74).
Fig. 5 *Glossopteris* seed in intact connection with the midrib of the leaf (specimen "B", cat.no. H I 99).
Fig. 6 Enlarged picture of the *Glossopteris* seed in intact connection with the midrib (specimen "B", cat.no. H I 99).

Palaeont. afr., **17**, 15—17 1974

A FOSSIL INSECT FROM THE DWYKA SERIES OF RHODESIA

by

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ABSTRACT

Hadentomoides dwykensis, gen. et sp. nov. (Paraplecoptera: Hadentomidae) is the oldest recorded insect in the southern hemisphere. It is similar to *Hadentomum americanum* from the Upper Carboniferous of North America. The close relationship between these two species tends to support the view that at least part of the Dwyka Series extends below the Permian into the Upper Carboniferous.

INTRODUCTION

The oldest insects hitherto described from the southern hemisphere are recorded from the Permian: none are recorded from the older, Upper Carboniferous, strata. The only extensive Permian fauna is that at Belmont, Australia, in sediments of Upper Permian age (Riek, 1968). A fauna of similar age (Middle Beaufort) is known to occur in South Africa (Riek, in press), and one of slightly older age in South America (Pinto, 1972b). Single species or limited faunas, comparable in age with these Upper Permian faunas, are recorded from Madagascar, the Falkland Islands (Tillyard, 1928) and Argentina (Pinto, 1972a). Handlirsch (1906—8) described a blattid from Kashmir: it was associated with a *Glossopteris* flora, and on this basis he inferred a Permian age for the species. Zeuner (1955) described a blattid, *Rhodesiomylacris bondi,* from the Lower Beaufort Series in Rhodesia, and Pruvost (1934) described a paraplecopteron, *Boutakovia salei,* from the base of the Ecca, the Series below the Beaufort, in the Democratic Republic of the Congo (formerly the Belgian Congo).

This paper records an insect from the Dwyka Series of Rhodesia. The Dwyka lies below the Ecca. The Series lies at the base of the Permian or top of the Upper Carboniferous or may extend across the time barrier between these two periods. As far as can be ascertained from the sometimes indefinite correlations between the freshwater sediments of the southern continents, this species from the Dwyka is apparently the oldest recorded insect in the southern hemisphere.

The single specimen was recovered from a bore core.

The species, represented by the well preserved apical half of a fore wing, is referred to the Paraplecoptera, the order that, almost certainly, forms the base order of the Neoptera. The wing venation is generalized, without fusions between any of the main veins. The archedictyon is partly reduced in this species but definitive cross veins have not developed from the irregular network.

SYSTEMATICS

ORDER PARAPLECOPTERA

FAMILY HADENTOMIDAE

The family is recorded from the Upper Carboniferous of North America. Carpenter (1965) synonymized this family, and the Palaeocixiidae, with the Protoperlidae, but the median field is more branched and the first branching is earlier in the Protoperlidae, including Palaeocixiidae, than in the Hadentomidae. The cross veins are irregular and tend to form a double row of cellules between the main veins, as in many Idelioidea, but the venation is relatively open. The unbranched vein in the middle of the wing is apparently the upper branch of M. CuA has several short apical branches directed to the posterior margin, as in Protoperlidae and Protembiidae.

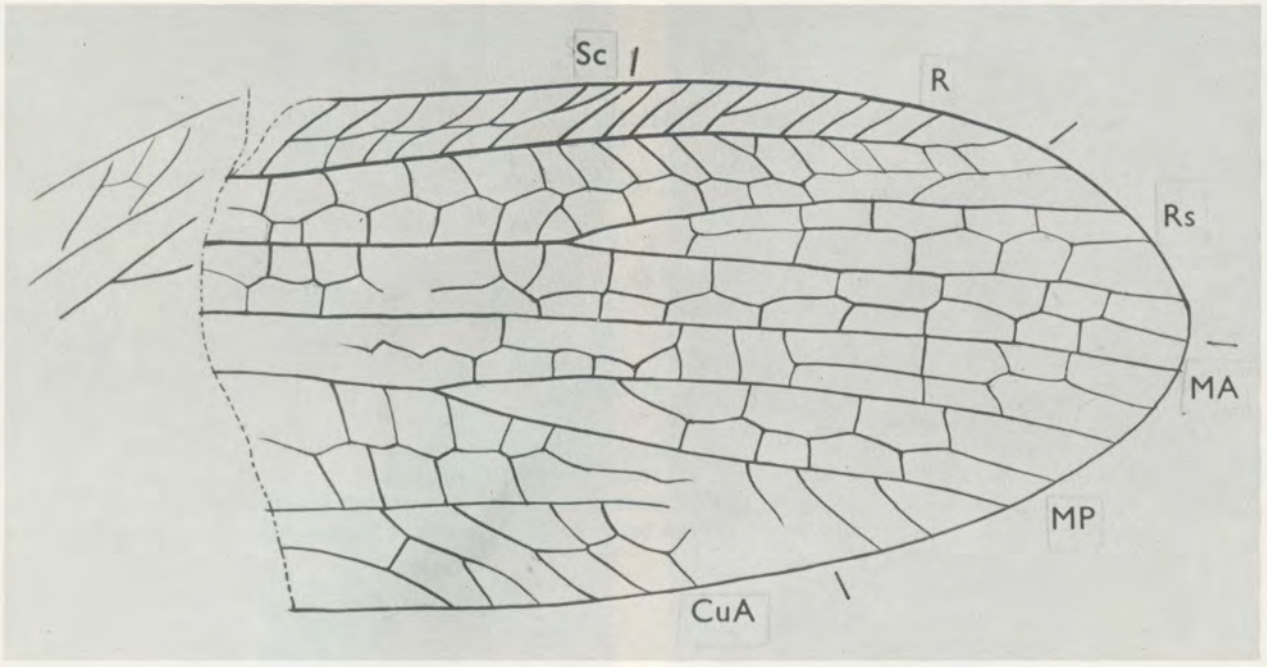
Genus *Hadentomoides* gen. nov.

Derivation: Hadentomoides = similar to *Hadentomum.*

Type species: Hadentomoides dwykensis sp. nov.

Diagnosis: Similar to *Hadentomum* but with a double row of cellules between all veins, at least in the apical (preserved) half of the wing. Rs 2-branched. M 3-branched, with terminal pectinate twigging on the posterior branch.

The genus resembles *Hadentomum* to a marked extent, and some of the apparent differences may be due to interpretation of the venation. For example, Rs may be only 2-branched in the fore wing of *Hadentomum* with a double row of cellules between Rs and M, as in *Hadentomoides.*



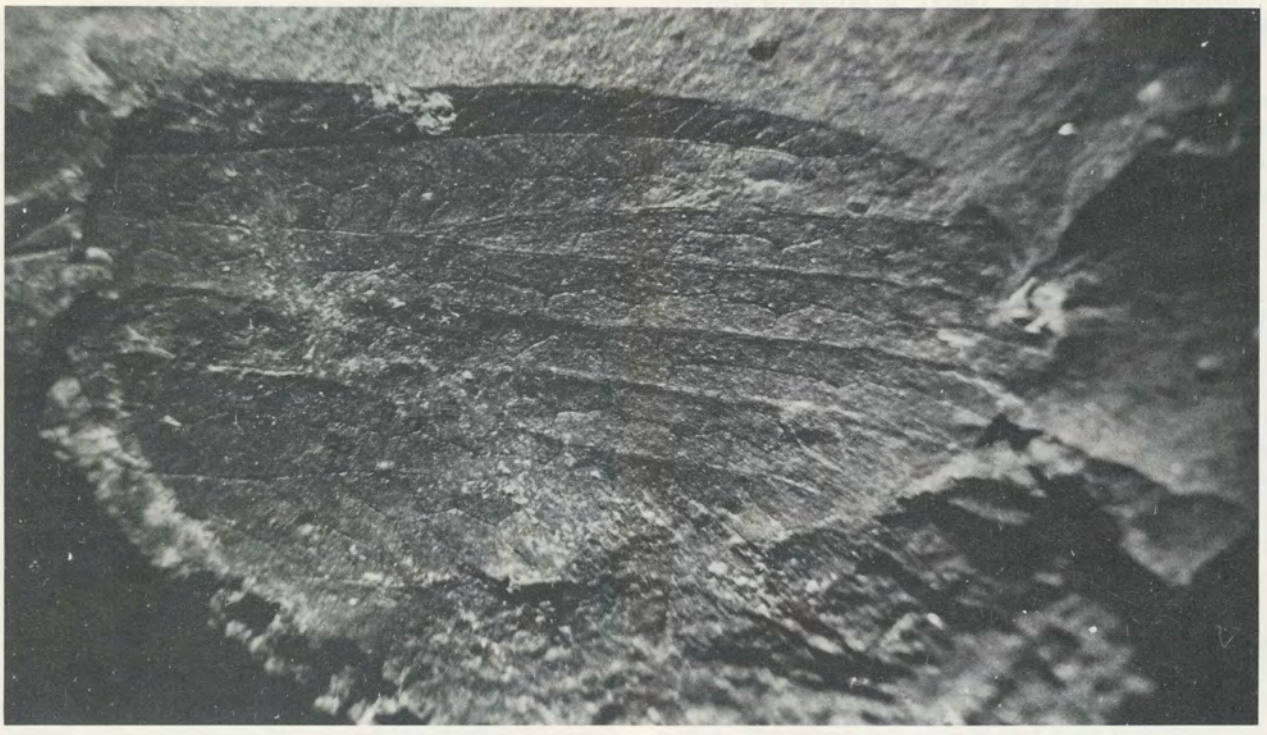


Fig. 1 *Hadentomoides dwykensis* sp. nov. Holotype X10 approximately.

Hadentomoides dwykensis sp. nov.
(Figure 1)

Derivation: dwykensis = from the Dwyka Series.

Type: Holotype in the Bernard Price Institute for Palaeontological Research, University of Witwatersrand, Johannesburg, South Africa. Counterpart, U.R. 10900, in the Geology Department, University of Rhodesia, Salisbury, Rhodesia.

Type Locality and Horizon. Matabola Flats, Rhodesia, Lat. 18° 07' S, Long. 27° 48' E. Depth in core approximately 880 feet (see Bond and Stocklmayer, 1967). Cycle 3, right at the top of the Dwyka succession in Rhodesia.

Description: Length of wing apex, as preserved, 12 mm ca.; width 7 mm. Sc extending well towards apex, but weak. R with numerous terminal twiggings to the costal margin. Rs 2-branched. MA simple. MP with two major branches, posterior branch with pectinate end-twigging. CuA with several terminal pectinate branches to the posterior margin, the stem of the vein subparallel to the margin, more as in *Protembia* than in *Hadentomum.*

Note: The species differs from *Hadentomum americanum* mainly in the terminal branching of M and more regular development of cellules in the wing.

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UPPER TRIASSIC INSECTS FROM THE MOLTENO "FORMATION", SOUTH AFRICA.

by

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ABSTRACT

Insects are recorded from eight plant fossil localities in the Molteno "Formation", but only heavily sclerotized species (Blattodea and Coleoptera) have been obtained from six of them. A small mecopteron was found at another locality, and only at Birds River, near Dordrecht, has a more diverse fauna, with representatives of the Orthoptera, ?Mantodea, Blattodea, Homoptera and Megaloptera, been obtained. The known fauna is closely comparable with the Triassic faunas of Australia.

Thirteen species, nine of which are described as new, are recorded from the Molteno. Six of the new species, and one described species, are referred to *Hagla, Mesorthopteron, Triassoblatta, Dysmorphoptiloides* and *Ademosyne,* genera represented in or previously restricted to the Australian Triassic faunas. The new monotypic genera, *Prosbolomorpha* (type species *clara:* Homoptera) and *Afristella* (type species *delicatula:* Mecoptera), are similar to genera recorded from the Triassic of Australia. *Euchauliodes distinctus,* gen. et sp. nov., is the earliest known Corydaloidean wing (Megaloptera); it is referred to a new family.

INTRODUCTION

Fossil insects are known from eight localities in the Molteno "Formation" (Upper Triassic), all of which are essentially fossil-plant localities.

The only previous record of insects from the Molteno "Formation" was from Upper Umkomaas, Natal where John Townrow made a large collection of plants during July—August 1956, and found a cockroach and three species of beetle (Zeuner 1961).

Since 1967, extensive plant fossil collections have been made by Heidi M. Anderson from 42 localities within the Molteno outcrop, and eight of these localities have yielded fossil insects. Five have yielded only single specimens whilst the remaining three, Little Switzerland (N-L.Sw.), Upper Umkomaas (N-U.U) and Birds River (C-Dt. II) have yielded 6, 14 and 45 specimens respectively.

A review of part of the Molteno flora with a map showing the distribution of localities and collecting data has been prepared by H. Anderson (1974, this journal). A review of the insect fauna found to date (January 1973) from the Molteno Formation is given in Table 1. In the present paper all the insects found prior to January 1973 and the single specimen from N-H1.II are described. The remaining insects, collected at Birds River (C-Dt. II) in January 1973, will be described in a subsequent paper.

The Triassic fauna from these localities in the Molteno Formation shows a close relationship to the Australian Triassic faunas of Mt. Crosby and Denmark Hill. A number of species are referred to genera recorded from Australia *(Hagla, Mesorthopteron, Triassoblatta, Dysmorphoptiloides* and *Ademosyne).* Most of the other species are similar to species recorded from the Triassic of Australia even though they are referred to distinct genera in the families Cicadoprosbolidae (Homoptera) and Mesopanorpodidae (Mecoptera). One species does not have comparable representation in the Australian fauna, but *Euchauliodes distinctus,* a megalopteron, represents the earliest known Corydaloid wing.

LIST OF FOSSIL INSECTS

Hagla contorta sp. nov.: Orthoptera.
Mesorthopteron similis sp. nov.: ? Mantodea.
Triassoblatta natalensis (Zeuner): Blattodea.
T. robusta sp. nov.: Blattodea.
T. sp.: Blattodea.
Prosbolomorpha clara gen. et sp. nov.: Homoptera.
Dysmorphoptiloides protuberans sp. nov.: Homoptera
Protopsyllidiid nymph: Homoptera.
Euchauliodes distinctus gen. et sp. nov.: Megaloptera.
Afristella delicatula gen. et sp. nov.: Mecoptera.
Moltenocupes townrowi Zeuner: Coleoptera.
Gen. et sp. indet. Cupedidae: Coleoptera.
Umkomaasia depressa Zeuner: Coleoptera.
Ademosyne speciosa sp. nov.: Coleoptera.
A. prisca sp. nov.: Coleoptera.
Gen. et sp. indet.: Coleoptera.
Pseudosilphites natalensis Zeuner: Coleoptera.

SYSTEMATICS
ORDER ORTHOPTERA
SUBORDER ENSIFERA
SUPERFAMILY GRYLLOIDEA
FAMILY HAGLIDAE

The family was recorded first from the Lower Triassic (Zeuner, 1939; Sharov, 1968). The fore wings of males are modified for stridulation. There is only a slight difference in venation between the sexes in *Prohagla superba* (Riek, 1954) from the Upper Triassic of Australia whereas the difference is pronounced in other species of the family. The South African species is referred to *Hagla,* a genus in which the fore wings are relatively long and narrow, and the median field is strongly arched in males, although the wing of the species from the Molteno is somewhat broader than in other species of the genus.

Genus *Hagla* Giebel, 1856.

Type species. Hagla gracilis Giebel.
Generic diagnosis. Fore wing long and rather narrow, with widened costal space. MA strongly arched in middle in fore wing of male. CuP and 1A very close, touching or almost touching one another, and strongly kinked in the middle.

Hagla contorta sp. nov.
(Fig. 1; Plate I, Fig. 1)

Derivation. Contorta from the complex venation of the male fore wing.
Type. C-Dt. II 351, Bernard Price Institute.
Type locality and horizon. Birds River, Dordrecht, Eastern Cape Province (C-Dt. II), Molteno Formation, Upper Triassic.
Description. Fore wing of male. Length, as preserved, 16 mm ca, indicating a wing length of 20 mm ca. Sc and R distinctly curved in middle. Rs arising at a very pronounced angle. Upper branch of MA strongly up-arched but distinctly separated from Rs, and branching secondarily just beyond its closest point to Rs. CuA_2 almost straight and diverging from CuA_1 throughout its length. Apices of CuP and 1A not clearly preserved, approaching one another in middle but apparently not touching one another. Precostal space distinct but relatively small.
Note. The species differs from those previously described in the broader costal space, the up-arching of Sc and R about the middle of the wing and absence of fusion at a point of CuP and 1A at the point of up-arching. It can be compared most closely with *Hagla sinuata* (Riek, 1955), from the Upper Triassic of Mount Crosby, Australia.

ORDER ? MANTODEA

The first undoubted mantids are the undescribed species from the Lower Cretaceous or Upper Jurassic of Transbaikal (Sharov, 1968) although the Upper Carboniferous Eucaenidae may be referable to the order. The Mesorthopteridae from the Triassic of Australia may also be Mantodea but, unfortunately, they are imperfectly known.

FAMILY MESORTHOPTERIDAE

This family has the unusual development of a series of forwardly-directed pectinate branches on CuA. The Strephocladidae from the Upper Carboniferous of the Saar and the Strephoneuridae from the Lower Permian of Tshekarda have a similar development but, as all are imperfectly known, ordinal placements remain in doubt. A reconstruction of *Mesorthopteron* was given by Tillyard (1922), but appears to be inaccurate.

M is not connected to CuA by a distinct cross connection in the Mesorthopteridae, and, in this respect, the species resemble Paraplecoptera and Mantodea. The irregular archedictyon also suggests relationship to the early Paraplecoptera and the Mantodea, and some Recent Orthoptera. There was apparently a small but not sharply defined clavus, with the margin of CuP straight.

Genus *Mesorthopteron* Tillyard, 1916

Type species. Mesorthopteron locustoides Tillyard 1916 : 14.
Generic diagnosis. Costal space broad. Sc extending almost to apex of wing, with numerous forwardly-directed branches. Upper branch of M forking distally.

Mesorthopteron similis sp. nov.
(Fig. 6; Plate I, Fig. 4)

Type. C-Dt. II 354 a, b, Bernard Price Institute.
Type locality and horizon. Birds River, Dordrecht, Eastern Cape Province (C-Dt. II), Molteno Formation, Upper Triassic.
Description. Incomplete wing. Length, as preserved, 22 mm, indicating a total length of 35—40 mm. Similar to *Mesorthopteron locustoides,* from the Triassic of Australia, but branches of Sc more regular and more oblique, and CuA and CuP more widely separate in middle.
Note. The slight difference between this species from southern Africa and *locustoides* from Australia may be no more than individual variation.

ORDER BLATTODEA
FAMILY POROBLATTINIDAE

Sc is distinctly branched although relatively short, and CuA relatively unspecialized, being in part dichotomously branched.

Genus *Triassoblatta* Tillyard 1919

Rhipidoblattopsis Zeuner 1961 (syn. nov.)
Type species. Triassoblatta typica Tillyard 1919 : 368.

Zeuner placed *Rhipidoblattopsis* (type species *Rhipidoblattopsis natalensis* Zeuner 1961) in the Mesoblattinidae. He was of the opinion that the genus was more closely related to the Liassic species of Europe than to *Triassoblatta* and *Samaroblatta* from the Upper Triassic of Australia. He stated that it was similar to *Rhipidoblattina* Scudder from the Liassic of Britain, especially in the sigmoidal curvature of the

branches of CuA but was distinguished by the slightly concave curvature of the branches of R towards the fore margin. Additional material of the species shows that it is very similar to species of *Triassoblatta* recorded from Australia, and *Rhipidoblattopsis* is here synonymized with *Triassoblatta*.

Triassoblatta natalensis (Zeuner)
(Fig. 2; Plate I, Fig. 2)

Rhipidoblattopsis natalensis Zeuner 1961 : 305
Type. In. 59529, British Museum (Natural History).
Type locality and horizon. Burnera Water Fall, Upper Umkomaas, Natal (Locality N-U.U.), Upper Triassic, Molteno Formation.
Description. Length of holotype tegmen, as preserved, 14,2 mm, indicating a total length of ca. 15 mm. Length of a second specimen (N-U.U. 411) 16,8 mm, width 5,3 mm. Costal space narrow, with an oblique groove from base that crosses the first two branches of Sc. Sc with six terminal branches. Sc ending slightly before level of apex of clavus. Claval veins, except first two, not looped, with seven veins in clavus. CuA with a slight tendency to pectination of its branches.
Note. Sc has more terminal branches than in most Australian species of the genus but this is probably somewhat variable even within a species, as is branching of most veins.

N-U.U. 671 a, b is probably another specimen but there are apparently 11 branches in the clavus.

Triassoblatta robusta sp. nov.
(Fig. 3; Plate II, Fig. 2)

Type. C-As. I 160, Bernard Price Institute.
Type locality and horizon. Askeaton, Eastern Cape Province (C-As. I), Molteno Formation, Upper Triassic.
Description. Length, as preserved, 10 mm indicating a total length of ca. 14 mm. Costal space broad, with an oblique groove from base that crosses the first four branches of Sc. Sc with six terminal branches. Sc ending level with apex of clavus. Clavus with probably seven veins, second and third looped just before margin, a very wide gap between first and second veins in more than basal half. R sigmoidally curved. M branching rather distally, level with apex of clavus.
Note. This species differs from *natalensis* in the venation of the clavus, shape of R, and wider costal space.

Triassoblatta sp.
(Plate II. Figs. 3, 4)

Specimen N-L.Sw. 349 from Little Switzerland, Oliviershoek Pass, Natal, is too imperfectly preserved for naming but it differs from the described southern African species in the number and branching of the veins in the clavus, and, to some extent, in the branching of CuA. Base of wing not preserved, complete from middle of clavus to apex of wing. Length, as preserved, 15 mm. R and M similar to *natalensis*. CuA partly dichotomously branched. Clavus with 13 or 14 branches at margin, third and fourth veins apparently branched, first vein moderately widely separated from claval margin over basal portion, as far as preserved.

Blattodea *incertae sedis*

N-L.Sw. 1006 a, b, from Little Switzerland, Oliviershoek Pass, Natal, is an almost complete fore wing but details of the venation are indistinct over the critical areas. It is apparently similar to, if not conspecific with, *T. natalensis*.

N-L.Sw. 1005; N-L.Sw. 459 and O-Za. I 28, from Zastron, Orange Free State, are very fragmentary blattid remains.

ORDER HEMIPTERA
SUBORDER HOMOPTERA
DIVISION AUCHENORRHYNCHA
FAMILY CICADOPROSBOLIDAE

Genus *Prosbolomorpha* gen. nov.

Type species. *Prosbolomorpha clara* sp. nov.
Diagnosis. Similar to *Austroprosbole* (Evans, 1943) but M_{3+4} branching almost from its point of origin from M, and CuA_1 directed towards apex of wing.

Prosbolomorpha clara sp. nov.
(Fig. 10; Plate I, Fig. 3)

Type. C-Dt. II 3, Bernard Price Institute.
Type locality and horizon. Birds River, Dordrecht, Eastern Cape Province, (C-Dt. II). Molteno Formation, Upper Triassic.
Description. Wing complete except for extreme base. Length, as preserved, 19 mm indicating a total length of ca. 21 mm; width 8 mm. Veins strongly impressed. Ambient vein distinct, especially at apex. Nodal break on fore margin distinct, with definite re-entrant angle. CuA and M close at base.
Note. The venation is thick over most of the wing. The area of the costal space is not well preserved so that it is not possible to say whether cross veins were present in this area or not.

SUPERFAMILY CERCOPOIDEA
FAMILY DYSMORPHOPTILIDAE

The family is recorded from the Triassic of Australia and Upper Jurassic of central Asia (Evans, 1956). A new species of the genus *Dysmorphoptiloides* first recorded from Australia is described from the Triassic of southern Africa.

This is a very specialized family of the Cercopoidea, characterized by the marked re-entrant angle in the fore margin. Actually the wing shape is due to a prolongation of the central portion of the apex in the area covered by the median and radial fields. The initial stages in this prolongation are seen in some Eoscartarellidae, and there is variation in shape in the Dysmorphoptilidae. Ambient vein distinct.

Genus *Dysmorphoptiloides* Evans, 1956

Type species. Dysmorphoptiloides elongata Evans 1956 : 219.

Diagnosis. Costal space with distinct cross veins. M four-branched. R with two or three branches to the wing margin beyond the re-entrant angle in fore margin. Rs just touching R or connected to it by a cross vein near its middle.

The two described species differ in the proportions of the apical wing lobe and in the connection between Rs and R.

Dysmorphoptiloides protuberans sp. nov.
(Fig. 9; Plate I, Fig. 5)

Type. C.Dt. II 342, Bernard Price Institute.

Type locality and horizon. Birds River, Dordrecht, Eastern Cape Province (C-Dt. II), Molteno Formation, Upper Triassic.

Description. Length, as preserved (only apex of wing), 11,5 mm. Similar to *D. parva* Evans (1956) from the Triassic of Australia in the relative size and shape of the apical wing lobe. R with three branches to the margin beyond the re-entrant in the fore margin. R and Rs connected by a cross vein. Cross vein between R and Rs and that between Rs and M almost in line.

Note. The whole of the wing membrane is thickened and sculptured. The ambient vein is distinct but close to the margin. The species differs from *D. parva* Evans only in the proportions between sections of the veins.

DIVISION STERNORRHYNCHA
FAMILY PROTOPSYLLIDIIDAE

The family is recorded from the Upper Permian and Triassic of Australia, Upper Triassic of Russia and Jurassic of Karatau. Nymphal exuviae have been recorded from Australia and Russia. A nymph is recorded from the Triassic of southern Africa, and is here described.

Protopsyllidiid nymph
(Plate I, Fig. 6)

Description. Complete nymph, C-Dt. II 1, Bernard Price Institute, from Birds River, Dordrecht, Eastern Cape Province. Molteno Formation, Upper Triassic. Length ca. 3 mm. Large wing-buds on mesonotum and metanotum. Head and prothorax apparently fused, although subdivision indicated at meson. Prothorax with median convex area and large paratergal lobes. Head portion apparently produced to form a continuous margin with prothorax, its anterior margin convex, and with a centrally raised area wider than median sections of thorax. Abdominal terga with distinct doublure, indicated by a marked lateral groove over whole abdomen.

ORDER MEGALOPTERA
SUBORDER EUMEGALOPTERA
FAMILY EUCHAULIODIDAE FAM. NOV.

Diagnosis. Differing from Recent Megaloptera in the basal origins of M and Cu, and greater number of cross veins. CuA two-branched. M four-branched. A number of cross veins between R and Rs. CuP arising close to base.

The family differs from Recent Chauliodidae not only in the basal origins of M and Cu but also in the number of cross veins between R and Rs, branching of M and branching of CuP. In the large number of cross veins between R and Rs it resembles the Neuromini and in the four-branched M it resembles *Platyneuromus* (Corydalini).

Genus *Euchauliodes* gen. nov.

Derivation. Euchauliodes = primitive *Chauliodes,* a Recent genus of the Order Megaloptera.

Type species. Euchauliodes distinctus sp. nov.

Diagnosis. CuP distinctly forked at apex. 1A and 2A widely separated throughout their lengths. Posterior branch of Rs deeply forked. M and CuA fused for only a very short distance, with the stem of M deflected towards CuA.

Euchauliodes distinctus sp. nov.
(Fig. 4; Plate II, Fig. 1)

Type. C-Dt. II 2, Bernard Price Institute.

Type locality and horizon. Birds River, Dordrecht, Eastern Cape Province (C-Dt. II), Molteno Formation, Upper Triassic.

Description. Fore wing, apex not preserved. Length, as preserved, ca. 28 mm indicating a wing of 35—40 mm; width ca. 11 mm. Three distinctly convex veins, R, CuA and Rs + MA_1. Costal and subcostal spaces appearing narrow through slight overfolding of convex R on to concave Sc. MA_1 separating from Rs before wing margin. Secondary branches of M close to margin. Branches of CuA directed somewhat towards wing apex. Anal veins distinctly swollen at base. Cross veins dense over most of wing.

ORDER MECOPTERA
FAMILY MESOPANORPODIDAE

The family is well represented in the Upper Permian and Triassic of Australia (Riek, 1953, 1956). The two known genera are separated on the development of the cubito-median Y-vein. A new genus is recorded from the Triassic of southern Africa. There is more fusion between M and CuA than in previously known species of the family and, in this respect, similarity to the Nannochoristidae, a family with extant species but also recorded from the Permian of Australia.

Genus *Afristella* gen. nov.

Derivation. Afristella = combination from Africa and *Choristella.*

Type species. Afristella delicatula sp. nov.

Diagnosis. Similar to *Prochoristella* (Riek, 1953) in wing shape, with narrow costal space, and in venation, except that the stems of M and CuA are fused for some distance towards base, and Sc and R touch at a point towards the apex of Sc.

Afristella delicatula sp. nov.
(Fig. 5; Plate I, Fig. 7)

Type. C-K.K. I 9, Bernard Price Institute.
Type locality and horizon. Konings Kroon, near Elliot, Eastern Cape Province (C-K.K.I), Molteno Formation, Upper Triassic.
Description. Length, as preserved, 4+ mm, indicating a fore wing length of ca. 5 mm. Costal space narrow. Subcostal space relatively wide. Both Rs and M four-branched. Rs_{1+2} forking after Rs_{3+4}. M not strongly arched at point of separation from CuA. Anal veins not adequately preserved but wing not markedly narrowed at base.
Note. This small wing would have been referred to the Nannochoristidae if Rs had been reduced to three branches, because of the marked fusion between the stems of M and CuA. It is also outstanding because of the close approximation of Sc to R at its apex, another character in which it resembles some Nannochoristidae.

ORDER COLEOPTERA
FAMILY CUPEDIDAE

Genus *Moltenocupes* Zeuner, 1961
Type species. Moltenocupes townrowi Zeuner 1961 : 304.

Moltenocupes townrowi Zeuner.
Moltenocupes townrowi Zeuner 1961 : 304.
Moltenocupes townrowi: Ponomarenko 1969 : 80.
Type. In. 59334 and paratype In. 59574, British Museum (Natural History).
Type locality and horizon. Burnera Water Fall, Upper Umkomaas, Natal (Locality N-U.U.), Molteno Formation, Upper Triassic.
Description. Length from head to tip of elytra 23 mm. The entire beetle, including mandibles, elytra and sternites (but not the tergites) coarsely punctate, with numerous small tubercles.
Note. Zeuner compared the species with the Recent Australian genus *Omma* from which it differs in the shape of the pronotum. However, Ponomarenko (1969) referred the species to the Triadocupedinae on its broad form and a pronotum that is antero-laterally produced.

Specimens N-U.U. 121 a, b and ?N-U.U. 402 a, b, from the Upper Triassic Molteno Formation, are tentatively referred to the species. They are very fragmentary and consist of only small portions of elytra. N-U.U. 1211 a, b, shows the rather pointed apex of an elytron that recalls those of the Permocupedidae. However, the number of rows of cellules in the wing is more in keeping with the Cupedidae. C-Rp. I C 100 a, b from Rooipoort, near Elliot, Eastern Cape Province, is an almost complete elytron probably referable to this species.

SUBFAMILY OMMATINAE
gen. et sp. indet.

Specimen from Little Switzerland, Oliviershoek Pass, Natal, N-L. Sw. 1028 a, b, Bernard Price Institute, is a complete insect preserved mainly in outline. The head is almost as broad as the pronotum, and the pronotum is apparently rounded antero-laterally. The species is similar in form to *Omma* (Cupedidae).

FAMILY PERMOSYNIDAE

Ponomarenko (1969) was of the opinion that the Permosynidae (syn. Ademosynidae) are on the cupedid line, and are also close to the ancestor of the Polyphaga. The sculpture of the elytra is reduced to lines of fine punctures.

Genus *Ademosyne* Handlirsch, 1906
Type species. Ademosyne major Handlirsch 1906.

Ademosyne speciosa sp. nov.
(Fig. 8; Plate I, Fig. 8; Plate II, Figs. 5 and 6)

Type. N-U.U. 1206 a, b and paratype N-U.U. 1208, Bernard Price Institute.
Type locality and horizon. Burnera Water Fall, Upper Umkomaas, Natal (N-U.U.), Molteno Formation, Upper Triassic.
Description. Length of elytron 9,5 mm; width 3 mm. Pronotum transverse, with antero-lateral margin rounded, postero-lateral margin slightly produced, and caudal margin slightly produced at meson; pronotum with fine sculpture, tending to be transversely rugose at meson. Scutellum visible at bases of elytra, but exposed area very small. Elytron long and thin, truncate at base, slightly pointed at apex. Elytron with eight faint longitudinal sulci. Sutural margin distinct, narrow; eighth sulcus very close to sutural margin, formed by fusion of two sulci close to base. Elytra very finely sculptured, finer than on the pronotum.

Ademosyne prisca sp. nov.
(Fig. 7; Plate II, Fig. 7)

Type. N-U.U. 1209, Bernard Price Institute.
Type locality and horizon. Burnera Water Fall, Upper Umkomaas, Natal (N-U.U.), Molteno Formation, Upper Triassic.
Description. Elytron length 9 mm. Elytron very convex, flattened in preservation so that sutural margin appears convex. Elytron with 11 fine sulci, seven clearly arising from base; posterior four arising as a unit; nine and ten joined at apex and the combined apex joined to 11th.

FAMILY ? PERMOSYNIDAE

Genus *Umkomaasia* Zeuner, 1961
Type species. Umkomaasia depressa Zeuner 1961 : 305.
Diagnosis. Zeuner did not give a generic diagnosis but the depression towards the base of the elytron on which he placed considerable emphasis is probably an artifact of preservation. Elytron with very numerous longitudinal carinae.

Umkomaasia depressa Zeuner
Umkomaasia depressa Zeuner 1961 : 305.
Type. In. 59564, British Museum (Natural History).

Type locality and horizon. Burnera Water Fall, Upper Umkomaas, Natal (Locality N-U.U.), Molteno Formation, Upper Triassic.
Description. Length slightly in excess of 8 mm; width 4 mm. Left elytron distinctly convex, with about 17 slight ridges separated by very fine grooves, every fourth or fifth ridge more pronounced.
Note. Zeuner compared the species with *Grahamelytron crofti* Zeuner (1959) from the Jurassic of Grahamland. He tentatively referred the species to the Carabidae on the depression towards the base of the elytron. The elytron resembles that of *Ademosyne* in shape but differs from this Triassic genus in the number of ridges.

FAMILY ? SILPHIDAE

Genus *Pseudosilphites* Zeuner, 1931

Type species. Pseudosilphites triassicus Zeuner 1931.

Pseudosilphites natalensis Zeuner 1961.

Type. In. 59573, British Museum (Natural History).
Type locality and horizon. Burnera Water Fall, Upper Umkomaas, Natal (Locality N-U.U.), Molteno Formation, Upper Triassic.
Description. Ventral view of whole beetle. Length 7,5 mm, width 5 mm. Pronotum large, semicircular, with head completely hidden beneath. Size of head proportionally smaller than in the Recent silphids, *Silpha obscura* L. and *Phosphuga atrata* L., which the species closely resembles, according to Zeuner.
Note. Family placement remains doubtful because of the inadequate preservation of the specimen.

ORDER COLEOPTERA

gen. et sp. indet.

Specimen N-U.U. 1905 a, b, Bernard Price Institute, is the ventral impression of the abdomen of an insect. N-L.Sw. 344 is possibly a beetle elytron. N-L.Sw. 347 is a small beetle elytron.
Note. An additional undetermined specimen was collected from Hlatimba Valley, Natal (N-H1. II).

TABLE 1

THE INSECT FAUNA OF THE MOLTENO FORMATION

Order Genus Species	Locality N-L.SW.	N-U.U.	N-Hl. II	C-K.K.I.	C-Rp. Ic	C-As. I	C-Dt. II	O-Za
Ephemeroptera (mayflies)								
1 gen. et sp. nov.							4	
(abdomen)							1	
Meganisoptera (protodragonflies)								
1 gen. et sp. nov.							1	
Odonata (dragonflies)								
2 gen. et sp. nov.							8	
Plecoptera (stoneflies)								
1 gen. et sp. nov.							1	
Orthoptera (grasshoppers)								
Hagla contorta sp. nov.							1*	
? Mantodea (mantids)								
Mesorthopteron similis sp. nov.							1*	
Blattodea (cockroaches)								
Triassoblatta natalensis Zeuner		3*						
T. robusta sp. nov.						1*	10	
T. sp.	1*							
Samaroblatta sp.							1	
incertae sedis	3*							1
(abdomen)							2	
Homoptera (cicadids etc.)								
Prosbolomorpha clara sp. nov.							1*	
Dysmorphoptiloides protuberans sp. nov.							1*	
3 gen. et sp. nov.							3	
Protosyllidiid nymph							1*	
Megaloptera (adlerflies)								
Euchauliodes distinctus sp. nov.							1*	
Mecoptera (scorpionflies)								
Afristella delicatula sp. nov.				1*				
Coleoptera (beetles)								
Moltenocupes townrowi Zeuner		4*			1*			
Ademosyne speciosa sp. nov.		2*						
A. prisca sp. nov.		1*					3*	
Umkomaasia depressa Zeuner		1*						
Pseudosilphites natalensis Zeuner		1*						
gen. et sp. indet.	2*	1*						
Incertae sedis			1*				4	
January 1973, totals for each locality	6	13	1	1	1	1	44	1

* Asterisk—described in this paper.

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FIGURES

Figure 1. *Hagla contorta* sp. nov. Holotype C-Dt. II 351.
Figure 2. *Triassoblatta natalensis* (Zeuner) Specimen N-U.U. 411.
Figure 3. *Triassoblatta robusta* sp. nov. Holotype C-As. I 160.
Figure 4. *Euchauliodes distinctus* gen. et sp. nov. Holotype C-Dt. II 2.
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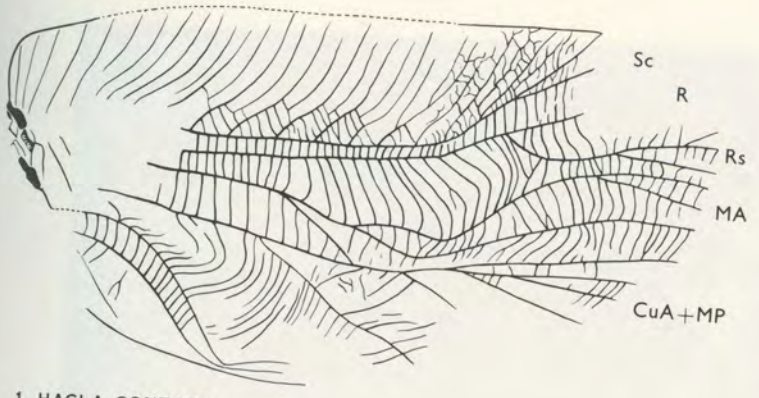
Figure 9. *Dysmorphoptiloides protuberans* sp. nov. Holotype C-Dt. II 342.
Figure 10. *Prosbolomorpha clara* gen. et sp. nov. Holotype C-Dt. II 3.



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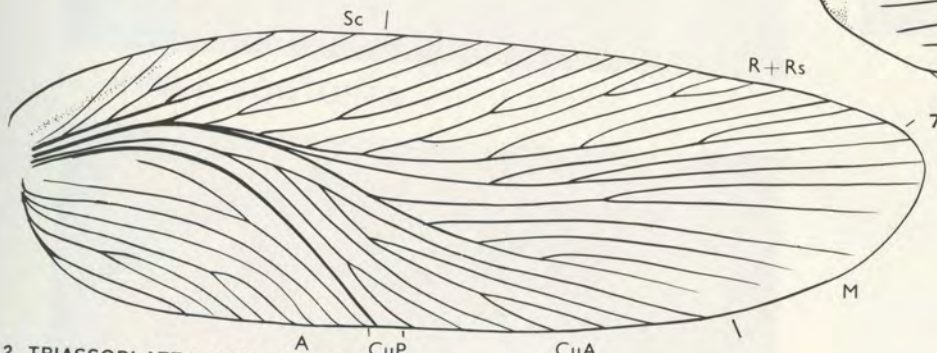

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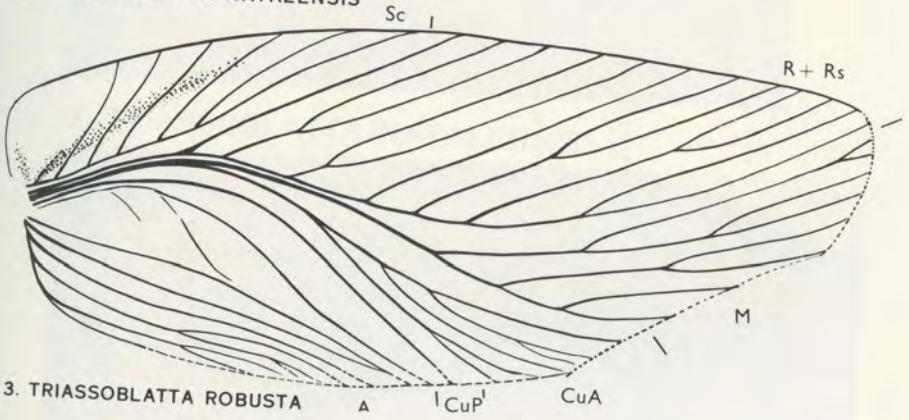

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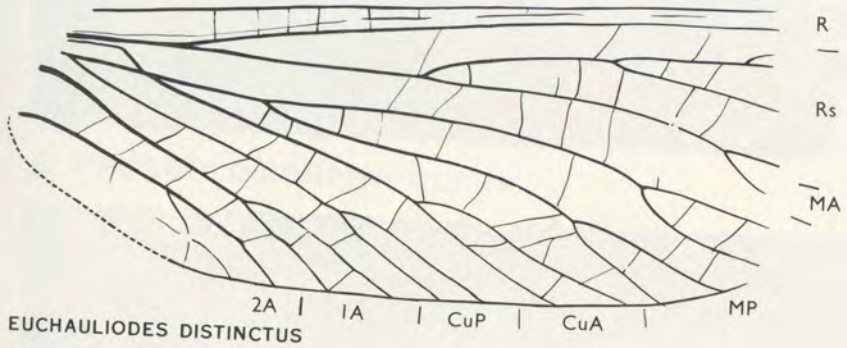

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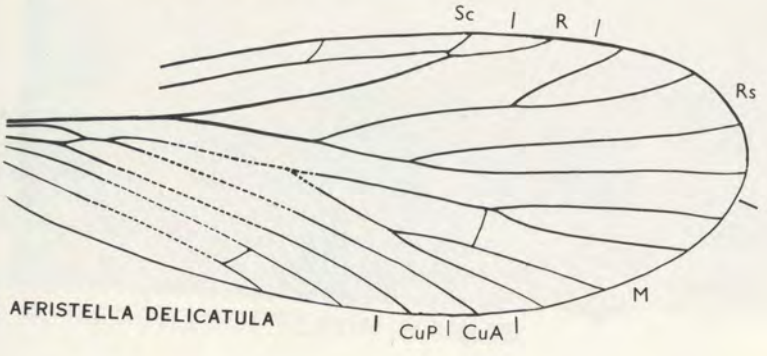

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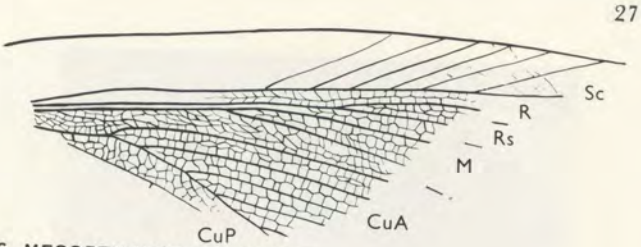

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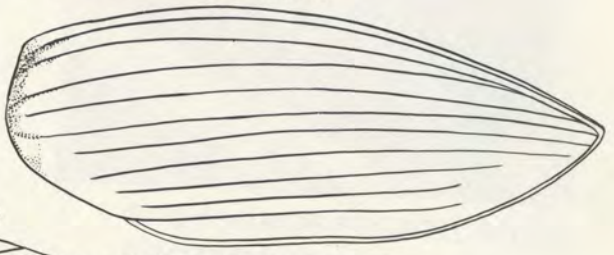
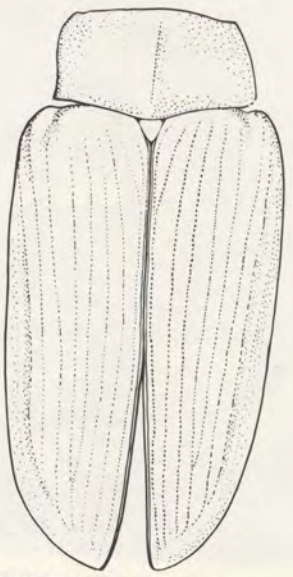


7. ADEMOSYNE PRISCA



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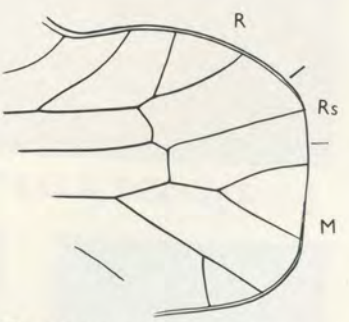
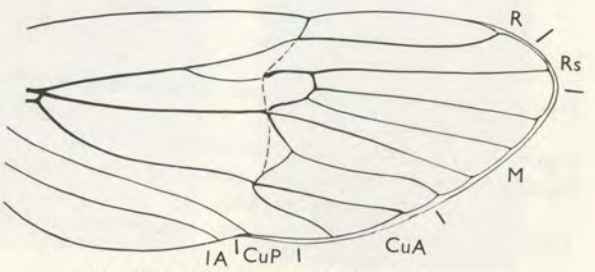


9. DYSMORPHOPTILOIDES PROTUBERANS



10. PROSBOLOMORPHA CLARA

PLATE I

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Figure 8. *Ademosyne speciosa* sp. nov. Holotype N-U.U. 1206 a. (Mag. 5X).



1. HAGLA CONTORTA



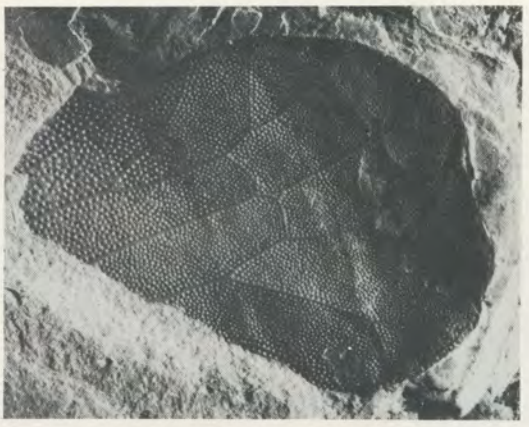
2. TRIASSOBLATTA NATALENSIS



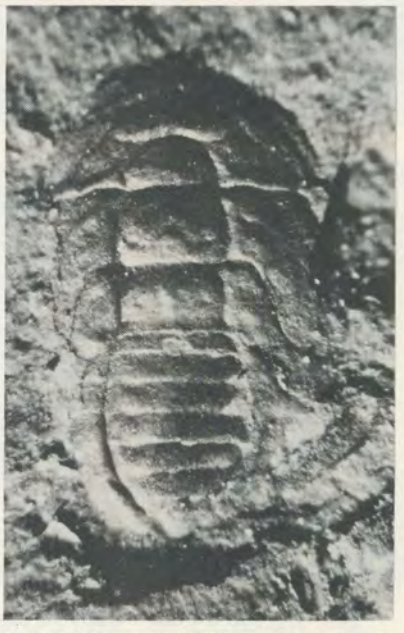
3. PROSBOLOMORPHA CLARA



4. MESORTHOPTERON SIMILIS



5. DYSOMORPHOPTILOIDES PROTUBERANS



6. PROTOPSYLLIDIID NYMPH



7. AFRISTELLA DELICATULA



8. ADEMOSYNE SPECIOSA



PLATE II

Figure 1. *Euchauliodes distinctus* gen. et sp. nov. Holotype C-Dt II 2. (Mag. approx. 6X).
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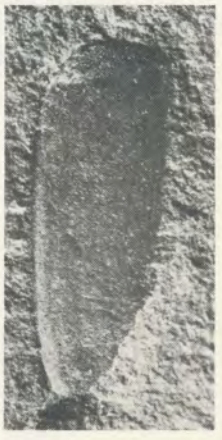
Figure 10. *Moltenocupes townrowi* N-U.U. 1211 b. (Mag. approx. 6X).

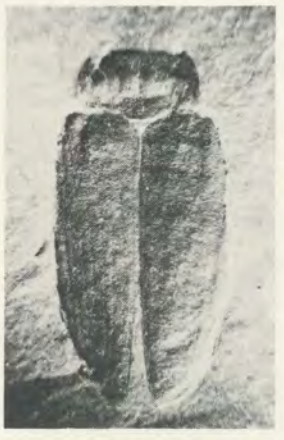


1. EUCHAULIODES DISTINCTUS



2. TRIASSOBLATTA ROBUSTA

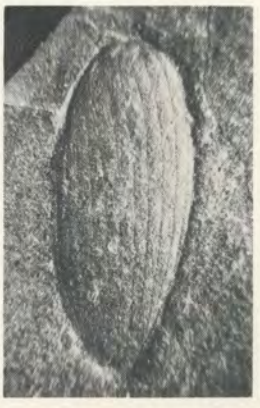




5. ADEMOSYNE SPECIOSA 6.



3. TRIASSOBLATTA SP.





7. ADEMOSYNE PRISCA 8. OMMATINAE



4. TRIASSOBLATTA SP.





9. ? MOLTENOCUPES TOWNROWI 10.

Palaeont. afr., **17**, 29—55 1974

CAPITOSAURID AMPHIBIANS FROM THE UPPER LUANGWA VALLEY, ZAMBIA

by

Sharon Chernin

ABSTRACT

The purpose of this paper is to describe two capitosaur skulls from the Luangwa valley, Zambia. A tentative decision is made assigning the material to *Parotosaurus pronus* (Howie, 1969).

The stratigraphy of the locality in which the material was found and that of the type species is discussed. A possible mechanism for opening the mouth of capitosaurs is put forward, with the qualification of its success depending on the animals being neutrally buoyant.

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INTRODUCTION

All the known members of the labyrinthodont family Capitosauridae were placed by Welles and Cosgriff (1965) in three genera: *Parotosaurus, Cyclotosaurus* and *Paracyclotosaurus*. Chronologically the genera occur as follows: *Parotosaurus* in the Bunter and early Muschelkalk; *Cyclotosaurus* in the Upper Muschelkalk and Lower Keuper; and *Paracyclotosaurus* in the Upper Keuper.

Watson (1962, p. 261) listed a number of evolutionary trends of the capitosaurs through the Triassic. Among these were the following: an increase in size of the skull; a disproportionate increase in the length of the nasal region; and a tendency to enclose the otic notch—this latter character dividing the family into the Lower Triassic parotosaurs with open otic notches and the Upper Triassic cyclotosaurs with closed otic notches. The third genus of capitosaurs, *Paracyclotosaurus* from the Upper Triassic of New South Wales, was considered to have a closed otic notch, and a deep skull.

Howie (1969) distinguished *Parotosaurus pronus* of the East African Triassic from ten other described species by the shape and position of its tabular horn, which is expanded laterally towards the squamosal, so that the otic notch is semi-closed.

In 1970, I recorded the presence of a large capitosaur from the Upper Luangwa Valley, Zambia (Chernin and Cruickshank, 1970), tentatively assigning it to *P. pronus,* on the basis of the similar tabular horn.

The purpose of this paper is to describe the above specimen and a second capitosaur found a few metres away. This latter material, although lacking the crucial tabular horns, displays proportions and other characters so similar to *P. pronus* that it has also been tentatively assigned to that species.

STRATIGRAPHY

The capitosaur material herein described was collected from the Upper Horizon of the N'tawere Formation by Drysdall and Kitching in 1961.

The two skulls were found within a few feet of each other in Locality 15 (Drysdall and Kitching, 1963), which is situated south of the Sangu River 3½ miles west of Sitwe, in the Upper Luangwa Valley, Zambia.

The fossiliferous beds of Locality 15 consist of dark red soft mudstones with characteristic feldspathic grit bands, containing angular vein-quartz fragments. Towards the base of the beds, amphibians and molluscs are present. The molluscs have been identified as *Unio karooensis* (Drysdall and Kitching, 1963, p. 22). From the same locality, two cynodonts were also collected, the smaller perhaps belonging to the genus *Trirachodon* and the larger being a *Scalenodon*-like form resembling material described by Crompton (1955) from the Manda Beds of Tanganyika.

The type material of *Parotosaurus pronus* described and named by Howie (1969) was collected from Mkongoleko, Ruhuhu Valley, Tanzania, in the Manda Formation of East Africa, by F. R. Parrington.

The genus *Parotosaurus* is known to have lived during Lower to Lower-Middle Triassic times (Welles and Cosgriff, 1965; Chernin and Cruickshank, 1970).

Dixey (1937) correlated the N'tawere Formation with the Manda beds because of the common presence of *Unio karooensis,* which was an unreliable correlation because *Unio karooensis* is not a true zone fossil.

Crompton and Ellenberger (1957) described *Scalenodontoides macrodontes* from the Upper Molteno Beds of Basutoland, thus correlating not only the Manda and Molteno Beds of Basutoland, but also the N'tawere Formation and Red Marl of the Upper Luangwa Valley, but Turner (1972) believes that *Scalenodontoides macrodontes* comes from the Lower part of the Red Beds, in Lesotho, and not from the Molteno.

Dicynodont material described from the Manda Formation is remarkably primitive for correlation with the Molteno, comprising as it does *Kannemeyeria latifrons,* which animal is typical of the supposed Lower Triassic *Cynognathus* zone, and its suggested morphological antecedent *Tetragonias njalilus* (Cruickshank, 1967).

The rhynchosaur fauna from the Manda Formation is similar in many respects to that of the Middle Trias of Brazil.

The archosaurs in the Manda Formation are more advanced than those in the *Cynognathus* zone, in keeping with the progressive nature of the cynodonts.

Therefore, although the Manda Formation fauna in general is more advanced than that of the *Cynognathus* zone, it is not significantly so and must represent a stage following closely on it (Chernin and Cruickshank, 1970).

The N'tawere Formation contains two fossiliferous zones, the lower with *Diademodon rhodesiensis* among other *Cynognathus* zone-like forms, and an Upper (Red Marl) horizon which includes Locality 15. Locality 15 has yielded, so far, two specimens of *Parotosaurus pronus,* a gomphodont similar to the "advanced" Manda Formation genus *Scalenodon* and two genera of dicynodonts similar to the Middle Triassic Argentinian and Brazilian forms (Brink, 1963; Cox, 1969).

From these facts, it would seem that the "Red Marl" horizon of the N'tawere is largely equivalent to that of the Mkongoleko area of the Manda Formation and that both of these post-date the *Cynognathus* zone only slightly. The lower of the two N'tawere horizons may, in fact, be the same age as the *Cynognathus* zone, but much more information regarding its fossils is necessary before definite correlation is possible.

If the foregoing discussion is correct in its assumptions, and both the N'tawere Formation and the Manda Formation are of the Middle Trias, then they must be low in the Middle Trias, and the *Cynognathus* zone must be relatively high in the Lower Trias.

MATERIAL AND METHODS OF PREPARATION

The material studied was as follows:

Field No.	*Museum No.*	*Identity*	*Remarks*	*Specimen*
4221	*B.P.I 424	*Parotosaurus pronus*, Howie	Broken skull + left lower jaw	A
4223	*B.P.I. 414	*Parotosaurus pronus*, Howie	Broken skull	B

* Bernard Price Institute for Palaeontological Research.

Both specimens A and B were collected from Locality 15 (Drysdall and Kitching, 1963) of the N'tawere Formation.

Specimen A is part of a skull with the associated left jaw ramus. This ramus has been almost perfectly preserved, with the exception of the teeth which have been broken off, their stumps remaining in most cases.

The skull was greatly fragmented and encased in N'tawere Green and Purple Marls (Dixey, 1937). The majority of the fragments have been joined with Glyptal. Sutures were made more evident by painting with a 2% solution of hydrochloric acid. Large gaps in the skull are still present (see Fig. 1).

Of the palate, only the vomerine plate and cultriform process of the parasphenoid are present. A fragmented brain-case which defied detailed preparation differed so greatly from right to left side that it seems possible that pathological deformation occurred on the right side.

Specimen B is part of a skull without the lower jaw. The skull was also greatly fragmented and encased in the N'tawere Green and Purple Marls.

Glyptal was used to join the majority of the fragments. However, large gaps are still present, as in the other.

The skulls were prepared using Vibro-tool and dental mallet.

In the case of Specimen B, the material permitted cleaning of the dorsal surface and the ventral surface of the condyles and pterygoids. The ventral surface of the skull roof was not prepared, many specimens of *Unio karooensis* being encased there in black manganese salts, which proved resistant against both Vibro-tool and a weak solution of acetic acid. A stronger solution of acid caused decomposition of the bone.

Specimen B has been greatly distorted (see Fig. 6), making a direct assessment of the outline impossible.

The sutures in both skulls are not apparent, or are only just visible, due to the high degree of fragmentation.

Because of the uncertainty of the outline in Specimen B and the considerable lack of distinct sutures in both skulls, I have used information from both Welles and Cosgriff (1965) and Howie (1969) to reconstruct the animals. The figures appearing in Tables 1, 2 and 3 were taken from direct measurements of my reconstructions, in order to obtain more direct comparisons with the other reconstructed parotosaurs. Also, my written descriptions rest entirely on my reconstructions.

In Figure 11 the illustrations of the lower jaw in Specimen A have been reversed left for right.

For key to abbreviations used in this paper, see pages 50—57.

It is possible that the much wider snouts in this material are due to growth changes, but I have discounted this here, because of the extreme distortion these skulls seem to have undergone.

It should also be emphasized that both skulls described herein are considerably larger than the type material and hence, for all these reasons, the identification of the material is given as *Parotosaurus* cf. *pronus*.

DESCRIPTION OF MATERIAL

Diagnosis of Specimen A

Skull broad posteriorly (B : L approximately 81), (ratios from Welles and Cosgriff 1965) but tapers anteriorly (S : L approximately 40); skull deep posteriorly (H : B approximately 17,2); external nares elongate, lateral, long axes parallel to skull border; orbits close together, well posterior, oval, long axes parallel to midline.

Pineal foramen rectangular, just posterior to hind border of orbits; posterior skull border concave (K : C approximately 32); frontal and jugal enter orbital margin; supratemporal excluded from otic notch.

Exoccipitals barely exposed on palate; pterygoid with facet for jaw articulation.

Processus lamellosus of exoccipital present.

Lower jaw with large prearticular process.

Description of skull roof

Unless otherwise stated, the left side of the skull is discussed.

The superficial sculpture of the bones is characteristic of all capitosaurs. The centre of ossification of each bone displays an area of irregular pentagonal pits. From this central area, ridges and grooves radiate outwards. These longitudinal grooves are probably the regions of intense growth (Bystrow, 1935). Where growth is slow, transverse ridges are able to develop so that such bones consist mostly of pits (Welles and Cosgriff, 1965). The postorbital bones are exclusively pitted, while the preorbital bones have elongated ridges (see Fig. 1).

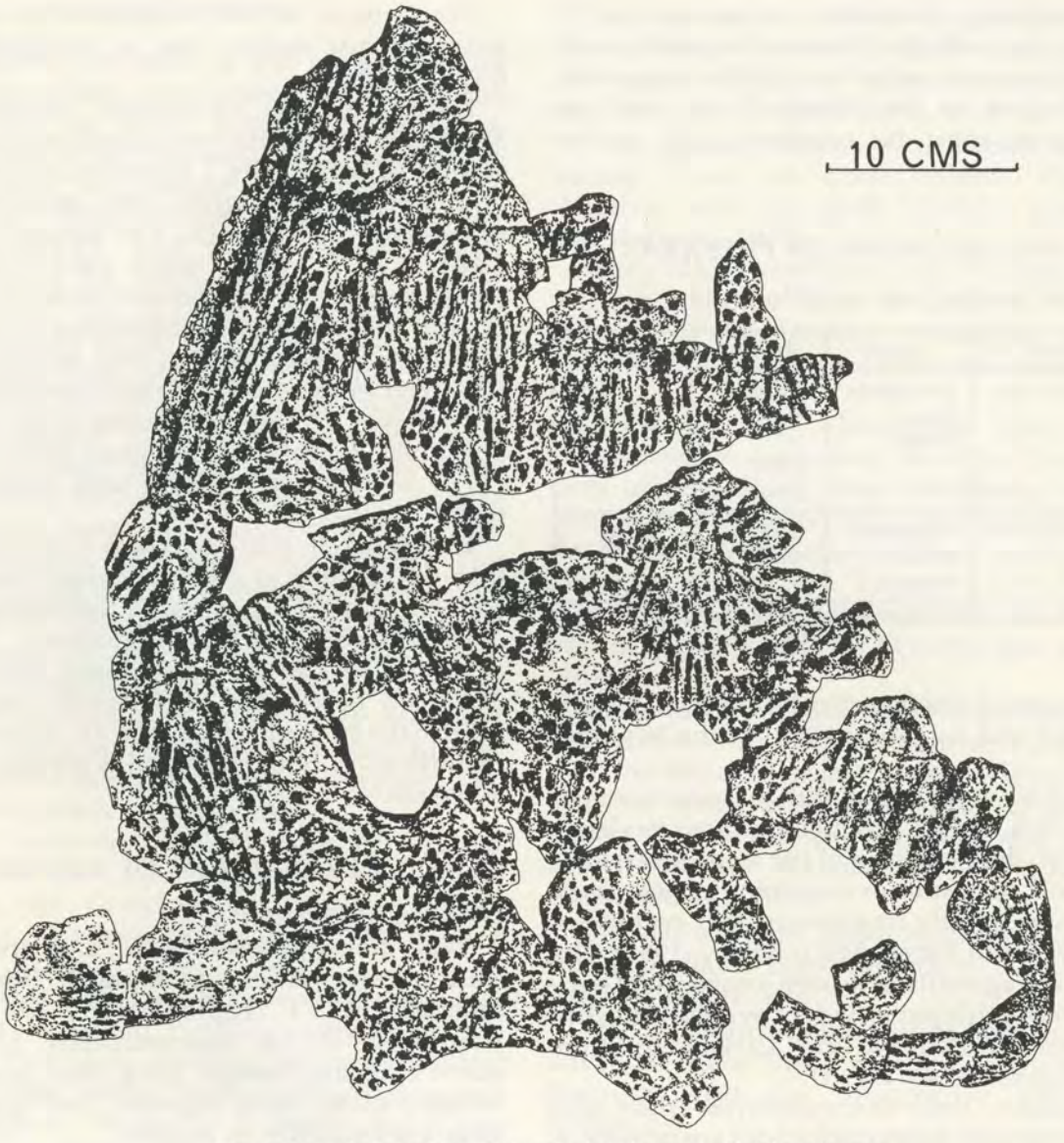


Fig. 1. Dorsal view of Specimen A, showing superficial sculpture.

KEY TO LINE DIAGRAMS

Solid line	—Visible outline or suture in estimated correct position.
Broken line	—Reconstructed outline or suture.
Double line of hooks	—Visible lateral line canal in estimated correct position.
Single line of hooks	—Reconstructed lateral line canal.
Heavy regular stipple	—Vacuity of foramen.
Light regular stipple	—Hollow or depression.
Parallel lines	—Worn broken surface.

For list of abbreviations used in text pages see pp. 54—55.

The preservation of a comparatively undamaged left maxilla shows that the skull was probably triangular with a rounded snout. The estimated length of the skull is 64,4 cm.

The superficial bones of the skull are seen in Figs. 1 and 2.

It should be noted that the supratemporal is excluded from the otic notch and that the frontal and jugal enter the orbital margin. Both of these characters are diagnostic (see Table 3).

Openings in the skull roof

No premaxillary foramen is seen, as the anterior tip of the skull is not preserved. For the same reason, no external nares are seen, except for a small region of hind border on the left hand side of the skull.

The orbits are probably oval. Only the posterior border of each orbit is smoothly rounded; the rest of the border has been shattered. The orbits are situated 10 cm apart in the posterior one-third of the skull. The long axes are probably parallel. The

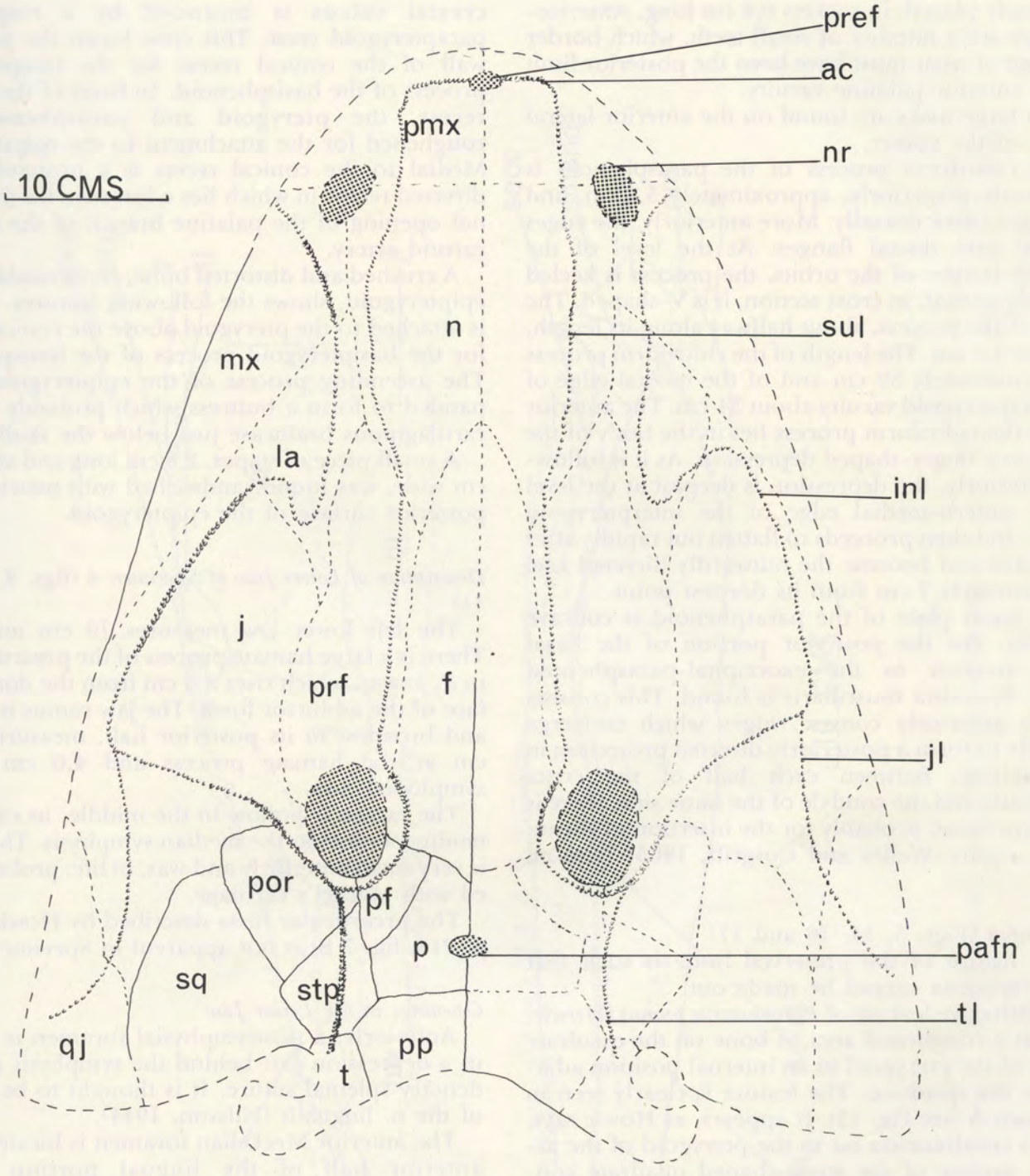


Fig. 2. Reconstruction and analysis of the dorsal view of Specimen A.

rim of the left orbit is raised slightly above the level of the skull so that a shallow groove between the orbits may have existed.

Where the parietal foramen probably existed, mostly a gaping hole now remains. A very small smooth edge is present, to show the approximate position of the foramen, but no shape can be made out.

The otic notch is clearly open, but the diagnostic tabular bone is missing. The skull is badly distorted in this area.

Lateral line system (Figs. 1 and 2)

It is possible to make out the 4 sets of canals on the skull roof. As the snout is missing, no anterior commissure can be determined.

The Palate (Figs. 4 and 12)

The vomerine plate forms a square flat platform about 11 cm long and 11 cm wide. Antero-laterally, this platform has a small smooth edge which probably is the antero-medial border of the choana. Internal to this edge are some small teeth,

alternately placed, in sockets 0,8 cm long. Anteriorly, there are a number of small teeth, which border the edge of what must have been the posterior limit of the anterior palatine vacuity.

Two large tusks are found on the anterior lateral corner of the vomer.

The cultriform process of the parasphenoid is quite wide posteriorly, approximately 5,2 cm, and the edges curve dorsally. More anteriorly, the edges develop into dorsal flanges. At the level of the anterior border of the orbits, the process is keeled ventrally so that, in cross section, it is V-shaped. The width of the process, about halfway along its length, is about 3,5 cm. The length of the cultriform process is approximately 39 cm and of the medial edge of the interpterygoid vacuity about 34 cm. The anterior end of the cultriform process lies in the body of the vomer as a finger-shaped depression. As it is followed posteriorly, the depression is deepest at the level of the antero-medial edge of the interpterygoid vacuity and then proceeds to flatten out rapidly after this point and become the outwardly directed keel approximately 7 cm from its deepest point.

The basal plate of the parasphenoid is concave ventrally. On the posterior portion of the basal plate, anterior to the exoccipital-parasphenoid suture, the crista muscularis is found. This consists of two anteriorly convex ridges which converge medially to form a posteriorly directed projection in the midline. Between each half of the crista muscularis and the condyle of the same side, there is a shallow fossa, probably for the insertion of the m. rectus capitis (Welles and Cosgriff, 1965; Watson, 1962).

The occiput (Figs. 5, 14, 16 and 17)

The nature of the preserved bone is such that small foramina cannot be made out.

A distinctive feature of *Parotosaurus pronus* (Howie, 1969) is a roughened area of bone on the quadrate ramus of the pterygoid in an internal position adjacent to the quadrate. The feature is clearly seen in Specimen A (see Fig. 13). It appears, as Howie says, to be a continuation on to the pterygoid of the articular surface of the screw-shaped quadrate condyle.

The Braincase (Fig. 15)

Such elements of the braincase as remain have been to a greater or lesser degree distorted. In fact, the right exoccipital is so badly out of shape that pathological deformation seems to have occurred.

Anterior to the base of the paroccipital process there is an oblique ridge which is the median edge of the fenestra ovalis. Antero-lateral to the basioccipital chamber is a deep recess formed by the parasphenoid in front and the exoccipital behind, known as the intercrestal sulcus. Laterally, the intercrestal sulcus ends at the pterygoid beneath the longitudinal ridge marking the fenestra ovalis in the dorsal groove of the pterygoid. Anteriorly, the intercrestal sulcus is bounded by a ridge, the parapterygoid crest. This crest forms the posterior wall of the conical recess for the basipterygoid process of the basisphenoid. In front of the conical recess, the pterygoid and parasphenoid are roughened for the attachment to the epipterygoid. Medial to the conical recess is a posterolaterally directed recess in which lies a foramen for the internal opening of the palatine branch of the internal carotid artery.

A crushed and distorted bone, recognisable as the epipterygoid, shows the following features. Its base is attached to the pterygoid above the conical recess for the basipterygoid process of the basisphenoid. The ascending process of the epipterygoid is expanded to form a buttress which probably met the cartilaginous braincase just below the skull roof.

A small piece of stapes, 2,8 cm long and about 0,9 cm wide, was found sandwiched with matrix to the posterior surface of the epipterygoid.

Description of Lower Jaw of Specimen A (figs. 9, 10 and 11)

The left lower jaw measures 70 cm internally. There is a large hamate process of the prearticular as in *P. pronus*, which rises 3,5 cm from the dorsal surface of the adductor fossa. The jaw ramus is highest and broadest in its posterior half, measuring 13,5 cm at the hamate process and 4,0 cm at the symphysial tusk.

The ramus is hollow in the middle, its cavity extending almost to the median symphysis. This cavity is very small anteriorly and was, in life, probably filled with Meckel's cartilage.

The prearticular fossa described by Howie (1969, p. 218, fig. 7 B) is not apparent in Specimen A.

Openings in the Lower Jaw

Anteriorly, a postsymphysial foramen is situated in a depression just behind the symphysis near the dentary-splenial suture. It is thought to be the exit of the n. lingualis (Nilsson, 1944).

The anterior Meckelian foramen is located in the anterior half of the lingual portion of the postsplenial, 19 cm from the postsymphysial foramen. It possibly served as the exit for the n. mylohyoideus anterior (Nilsson, 1944).

The posterior Meckelian foramen is bordered by the postsplenial antero-ventrally, the angular postero-ventrally and the prearticular dorsally. Only the ventral limit, smoothly rounded on the angular bone, remains to show the approximate size and position of this opening in this specimen. According to Nilsson (1944) the n. mylohyoideus posterior passes through it.

The adductor fossa is bounded lingually by the prearticular and laterally by the surangular. It is approximately 4 cm wide at its widest point, about half-way along its length, which is about 19 cm. The large adductor musculature of the jaw inserted here.

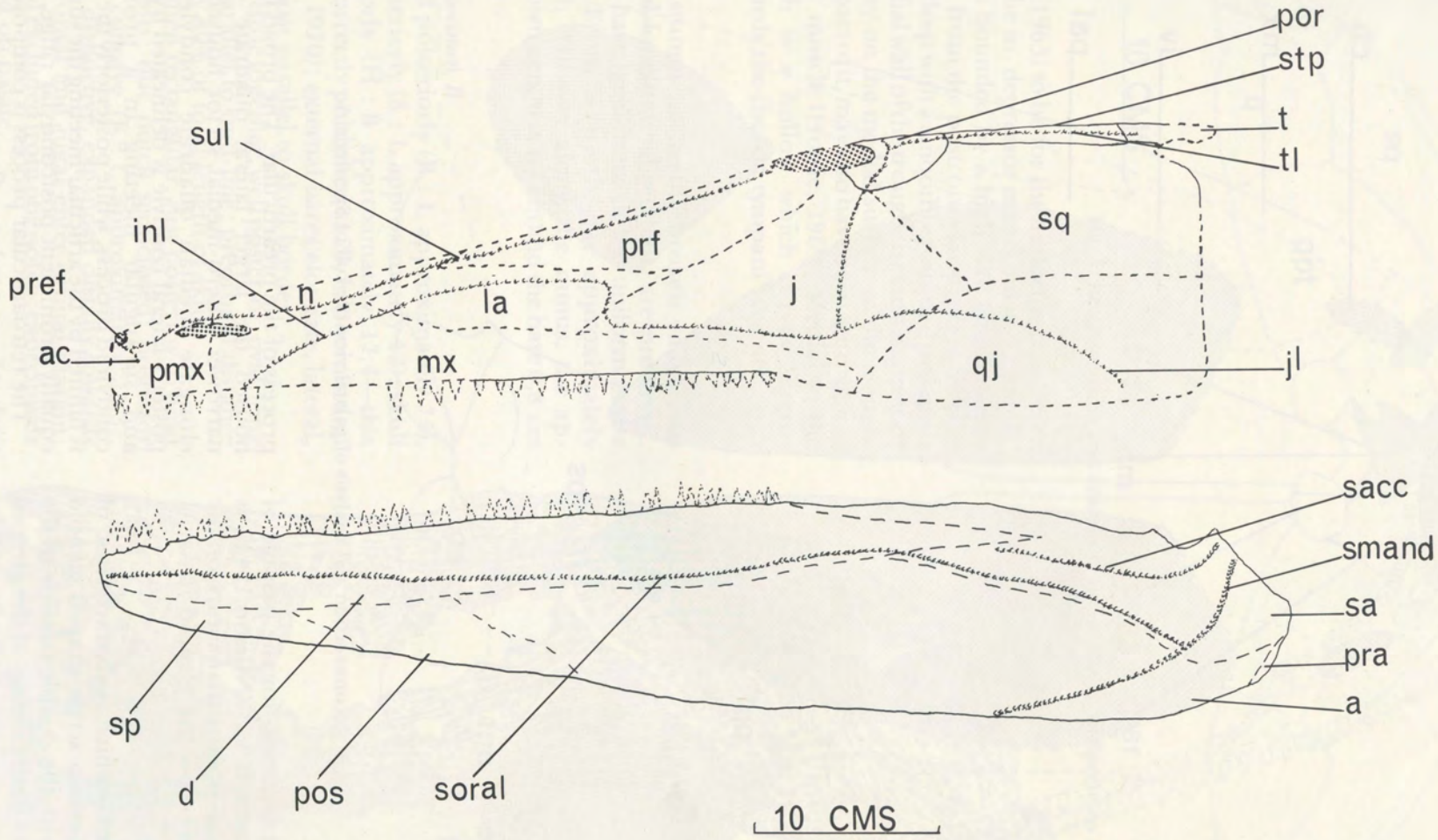


Fig. 3. Reconstruction of lateral view of Specimen A.

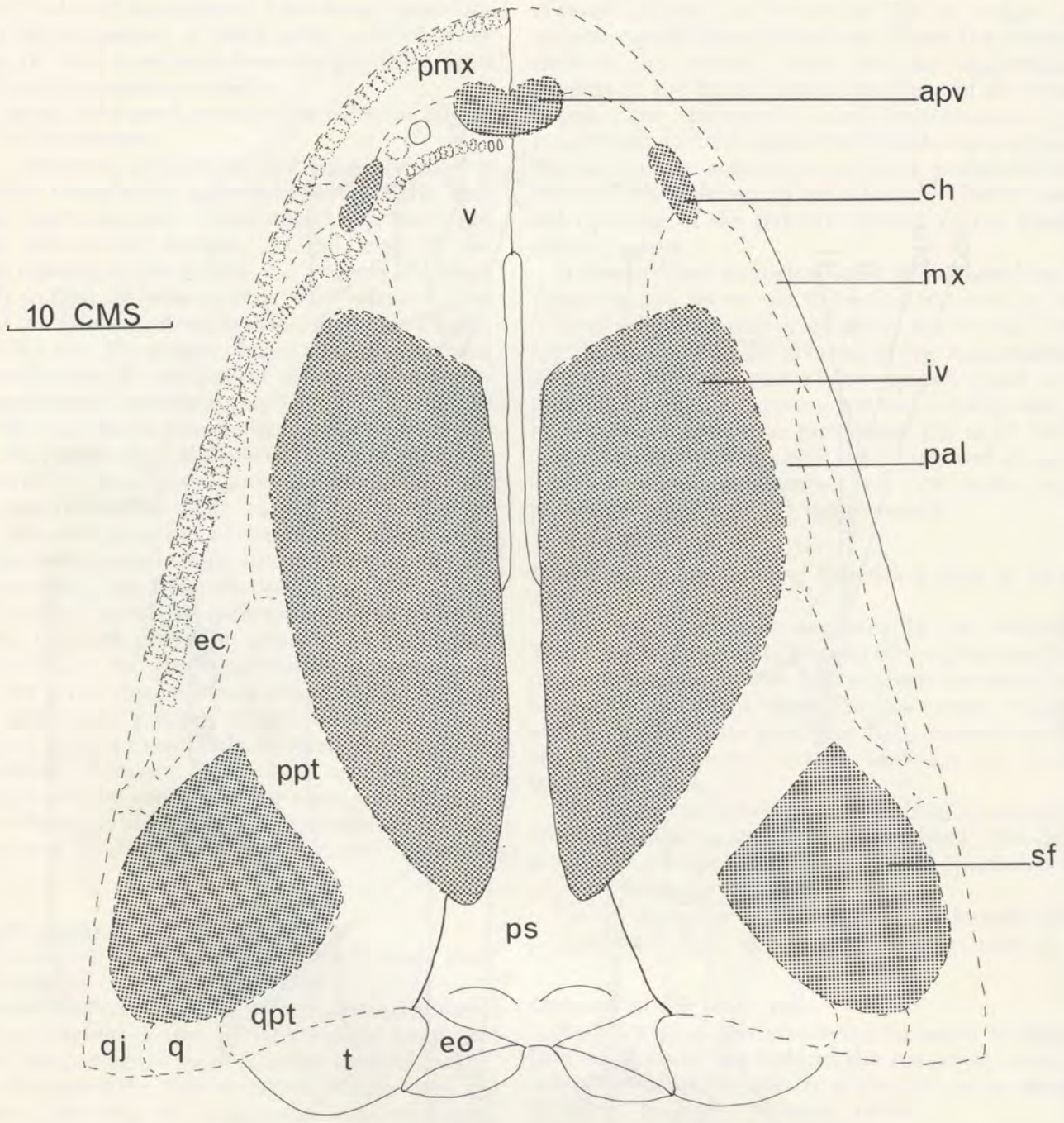


Fig. 4. Reconstruction and analysis of palatal view of skull of Specimen A.

The chorda tympani foramen, for the passage of the n. mandibularis internus VII (Nilsson,1944), is situated in the surangular-prearticular suture on the medial surface, 1,5 cm below the glenoid fossa.

Bones of the Lower Jaw

The articular is pitted—which is characteristic of cartilage bone—and forms a screw-shaped glenoid fossa for articulation with the double condyle of the quadrate. There are two distinct areas of the glenoid fossa: a broad transverse groove entirely formed by articular and a narrower, more median groove at an angle to and in front of the former, composed of articular and prearticular. The median groove is contained by the roughened posterior face of the hamate process of the prearticular. The broad lateral groove housed the larger lateral quadrate condyle; the narrower antero-medial sector housed the thinner elongate median quadrate condyle. The main postero-lateral condyle is delineated by the articular and surangular meeting in a prominent precondyloid process, while posteriorly the glenoid fossa is limited by the articular meeting the surangular at an equally prominent postcondylar ridge.

The retroarticular process is composed almost entirely of surangular; a flange of the angular extends along the ventral surface for about half of the length of the process to end in a sharp angle 1 cm anterior to the end of the jaw. The dorsal surface of the retroarticular process is occupied by a deep trough, said by Welles

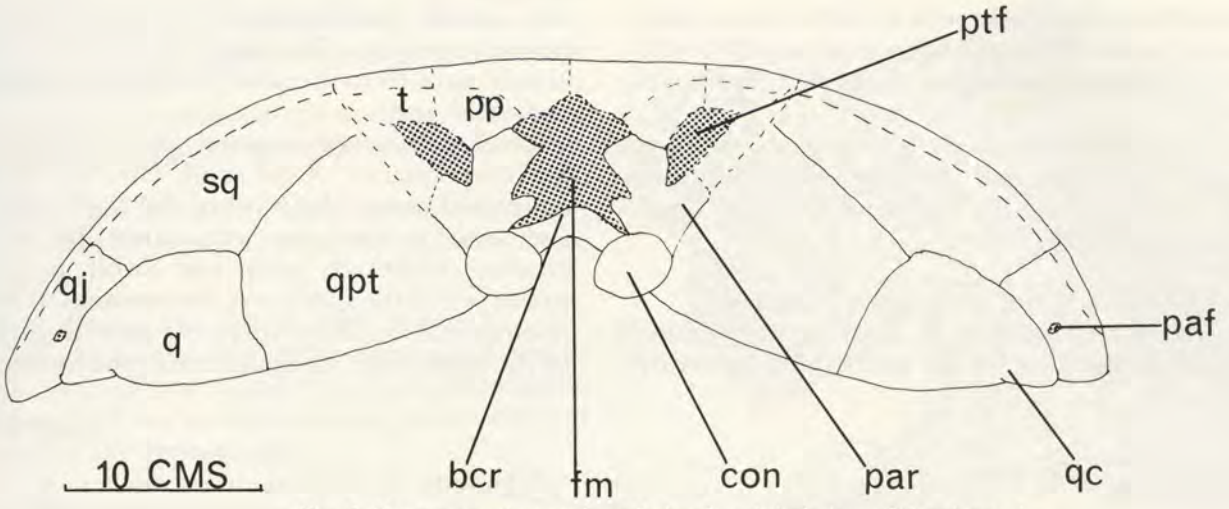


Fig. 5. Reconstruction and analysis of occipital view of Specimen A.

and Cosgriff (1965) to be for the adductor muscles of the jaw, viz. the m. depressor mandibulae. Laterally, this trough is bounded by a high wall which slopes down rapidly from the postcondylar process, so that the trough is deep with a smoothly rounded posterior wall. The medial wall of the trough rises to a sharp spur about half-way on the medial surface of the trough. This spur, or part of it, may also have been the origin of the depressor muscle (Howie, 1969). Medial to the dorsal trough is a hollow which curves antero-medially towards the chorda tympani foramen.

Teeth

Only the stumps of teeth, broken in various transverse and longitudinal sections, are preserved. They seem to have been more or less uniform in size and shape. From a tooth cut approximately longitudinally, half-way along the ramus, the approximate crown height is 1,7 cm and the base 0,8 cm wide.

Diagnosis of Specimen B

Skull broad posteriorly (B : L approximately 75), but tapers anteriorly (S : L approximately 42); skull deep posteriorly (H : B approximately 17,4—this figure was incorrectly published as 20, in Chernin and Cruickshank, 1970); external nares elongate, lateral, long axes almost parallel to skull border.

Orbits very close together, well posterior, oval, long axes almost parallel to mid-line; preorbital distance approximately 80% of total length of skull.

Pineal foramen rectangular, just posterior to hind border of orbits; otic notch semiclosed; posterior skull border concave (K : C approximately 19,3); tabular horns distinctive, expanded distally towards squamosal; frontal and jugal enter orbital margin; supratemporal excluded from otic notch; exoccipitals barely exposed on palate.

Description of skull roof of Specimen B (Figs. 6, 7 and 8)

The skull is greatly elongated in the preorbital region; the snout is rounded. As preserved, the shape



Fig. 6. Dorsal view of Specimen B.

of the skull is rectangular seen in dorsal view, due to the total absence of the quadrato-jugal and distortion whereby the jugal is pushed medially and overlaps the maxilla.

Only one half of the skull is preserved, with great gaps, bad distortion and virtually invisible sutures. The tip of the premaxilla is distorted so that the estimated length is 79,5 cm.

Openings in the skull roof of Specimen B

The external naris lies in the anterior one-eighth of the skull, surrounded by the premaxilla anteriorly, the nasal posteromedially and the maxilla posterolaterally. The naris lies with its long axis almost parallel to the skull border. It is elongated and oval in shape.

Oval orbits are situated close together in the posterior quarter of the skull. The rims of the orbits are raised above the level of the skull table, so that the two orbits are separated by a shallow groove. Although only one orbit is completely preserved in the specimen, the position of the other is distinguishable. Anteriorly, the orbital rim is formed by the prefrontal; medially first by the frontal and then

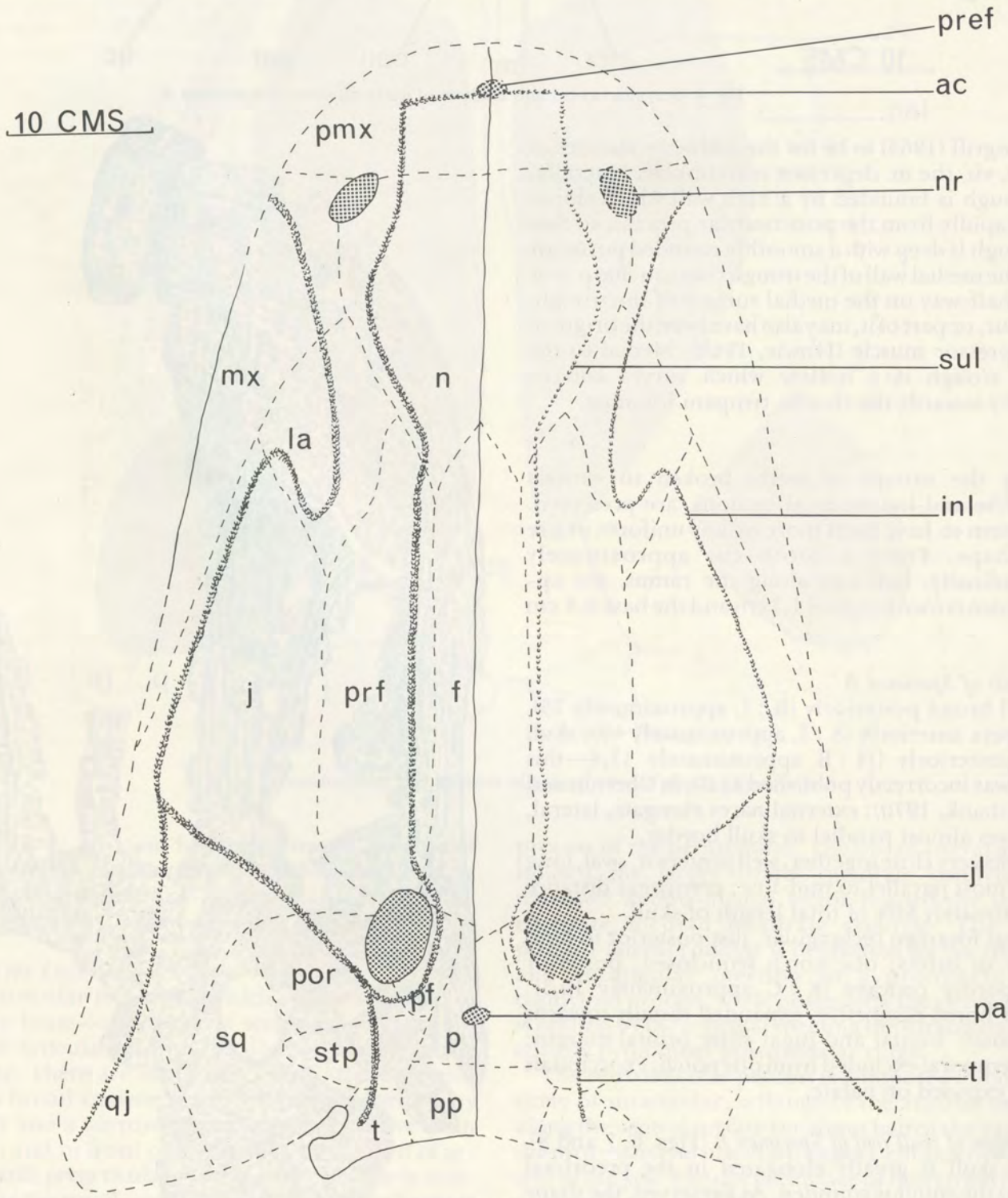


Fig. 7. Reconstruction and analysis of dorsal view of skull of Specimen B.

the postfrontal; anterolaterally first by the jugal and then, posterolaterally, the postorbital. The long axis of the orbit is slightly oblique, converging anteriorly towards the midline.

Close behind the orbits on the midline, in the centre of the parietals, lies the parietal foramen. It is rectangular.

The otic notch is oval in shape and the exterior meets via a narrow canal between the squamosal and tabular horn.

Lateral line system of Specimen B (Figs. 6 and 7)

As described by Moodie (1908) there are 4 sets of canals on the skull roof: jugal, temporal, infraorbital and supraorbital, the last three joining at the centre of ossification of the postorbital.

The course of the canals is distinctly marked by a series of enlarged pits and grooves.

Occiput of Specimen B (see Fig. 16)

Anterior to the dorsal and paroccipital process of the exoccipital only the more prominent structural features are visible. The left half of the dorsal occipital region and the right half of the ventral occipital region are preserved; thus the description is based on a combination of the two elements which not only are on opposite sides of the midline, but also lack visible sutures. This leads to a lack of continuation from the dorsal to the ventral elements.

Ventral surface of the occipital region

Only the basal plate of the parasphenoid is preserved together with crescent-shaped bars of the pterygoids.

The basal plate of the parasphenoid is bounded by oblique sutures to the pterygoid and, posteriorly, the parasphenoid has a slanted suture with the exoccipital. The parasphenoid has a small free margin in the posterior midline between the exoccipital condyles. Ventrally, the parasphenoid plate is concave.

The crista muscularis crosses the posterior portion of the basal plate of the parasphenoid transversely, just anterior to the exoccipital-parasphenoid suture. The crista muscularis consists of two anteriorly convex ridges which join medially to form a peaked posterior projection in the midline. Between each half of the crista muscularis and the condyle of the same side there is a shallow fossa, which is the pocket for the insertion of the rectus capitis muscle (Watson, 1962; Welles and Cosgriff, 1965).

The body of the pterygoid joins the parasphenoid in an oblique suture which issues from the centre of the posterior border of the interpterygoid vacuity and runs to the posterior margin of the skull just lateral to the exoccipital-parasphenoid suture. Anterolaterally, the palatine ramus of the pterygoid extends from the body of the pterygoid. The medial edge of this palatine process is the lateral border of the interpterygoid vacuity. The quadrate ramus of the pterygoid extends posterolaterally. The lateral edge of the palatine and quadrate processes of the pterygoid form the median rim of the subtemporal fenestra.



Fig. 8.
Dorsal view of otic notch of Specimen B, showing superficial sculpture.

Posterior view of the occiput

The paired exoccipital condyles face slightly inwards and downwards. The foramen magnum between the exoccipitals is the centre of the occiput proper. The tabulars form the dorsolateral corners of the occiput and the quadrate rami of the pterygoids dominate the lateral regions of the back of the skull.

Each exoccipital consists of a central condyle above which is a dorsal process and, lateral to the dorsal process, a paroccipital process. Each condyle is almost round and is surrounded by a raised ridge which is believed to have supported a cartilaginous cap.

Medially, the dorsal process forms the sloping dorsolateral limit of the foramen magnum. A lateral ridge of the dorsal process of the exoccipital forms the median border of the post-temporal fossa. The paroccipital process of the exoccipital rises beneath the post-temporal fossa to meet the tabular. The post-temporal fossa is bounded ventrally and laterally by the paroccipital process. The jugular foramen which transmits nerves IX and X opens externally in a foramen postero-latero-ventral to the paroccipital process. The external opening for the hypoglossal nerve XII is near the anterolateral edge of the condylar rim (neither foramen is seen in the illustrations.).

Between and below the exoccipitals is the parasphenoid. Posteriorly, the free margin of the parasphenoid is raised in the midline to form the basioccipital crest and in this region forms the floor of the chamber in which the cartilaginous basioccipital is believed to have been situated.

The tabular forms the dorsolateral corner of the occiput. The dorsal part of the tabular is the tabular horn. A thick arm of the tabular runs ventromedially to meet the exoccipital and sutures with the paroccipital process. A rugose area is present immediately below the distal end of the tabular horn. A prominent

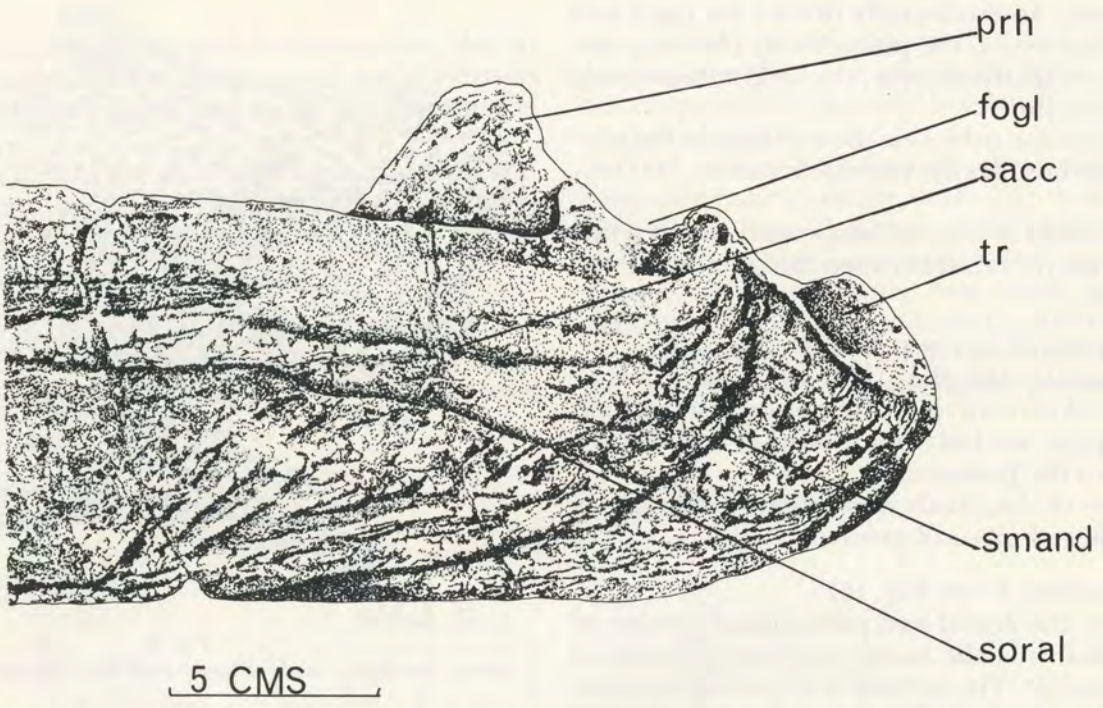
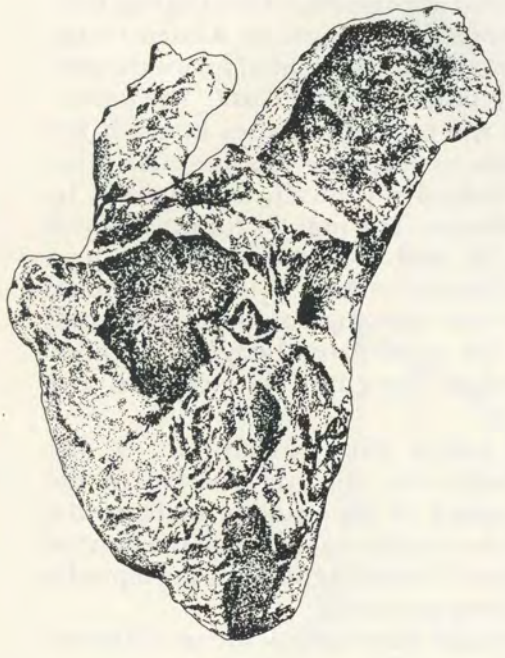


Fig. 9. Lateral view of posterior end of left lower ramus of Specimen A, showing lateral line complex.

FIG. 10 A.



10 B.

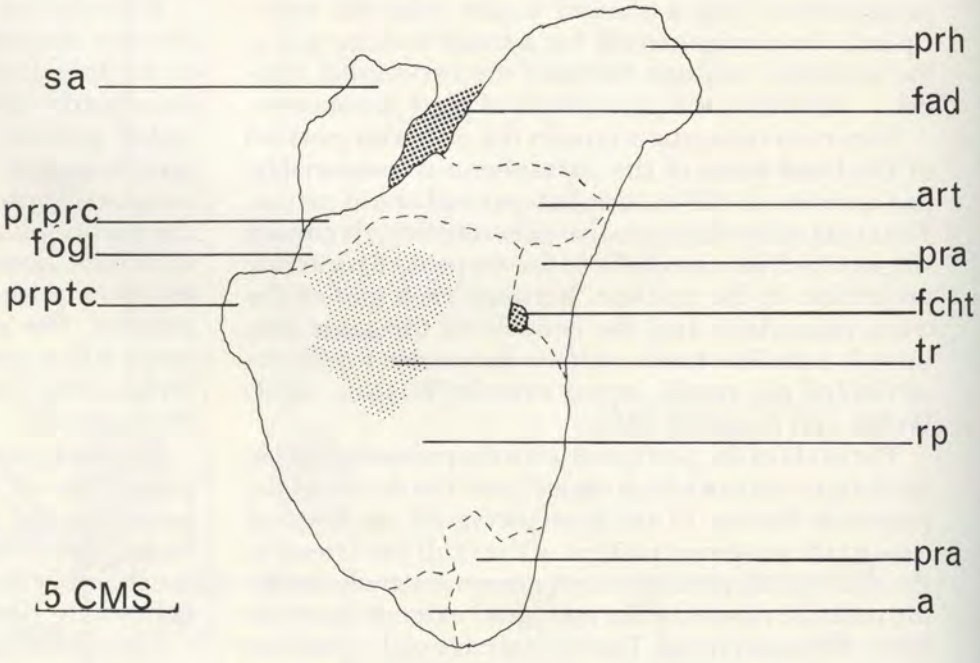


Fig. 10A. Posterior view of left lower jaw of Specimen A.

Fig. 10B. Analysis of posterior view of left lower jaw.

muscle ridge on the tabular runs posterolaterally along the paroccipital process. Just lateral to the exoccipital-pterygoid suture, the pterygoid curves anteriorly to form a cup-shaped region beneath the otic notch, the subtympanic cavity.

Teeth

No teeth have been preserved, but a few uniform tooth sockets are visible on the premaxilla and maxilla.

Table 1

Measurements of reconstructed skull
(N.B. The reconstructed skull is used to obtain measurements due to the large degree of distortion in the material.)

Specimen	A	B
	cm	*cm*
1. Height of postparietals above the parasphenoid (H)—	9,6	10,4
2. Breadth of skull across quadrates (B) ———	55,8	59,5
3. Length of skull (L) ———	64,4	79,5
4. Interorbital distance taken at mid-length of orbit (A) ———	10,4	7,0
5. Distance from tip of snout to level of anterior edge of orbit (O)———	45,4	60,5
6. Distance from level of posterior limit of orbit to level of centre limit of skull (D)———	12,5	11,5
7. Distance from postero-lateral corner of eye to otic notch (N) ———	10,4	9,5
8. Midline distance from centre posterior limit of skull to level of posterior limit of tabular horn (K) ——	5,6	3,0
9. Distance between otic notches (C) ———	17,5	15,5
10. Distance from mid-length of orbit to lateral edge of same side (I)	14,1	19,0
11. Distance from posterior mid-point of nare to anterior mid-point of orbit (F)———	34,1	48,5
12. Distance between nares at mid-length of same (J) ———	14,1	17,0
13. Distance from level of anterior limit of nares to edge of snout (M) ———	4,1	9,0
14. Breadth of snout 1/5th of skull length from tip (S) ———	25,8	33,5
15. Distance from level of posterior limit of orbit to parietal foramen taken at centre of skull (P)———	2,9	1,5
16. Midline distance from level of anterior limit of otic notch to parietal foramen (T)———	5,8	6,0

Table 2

Habitus Characteristics of Capitosaurs.
(Chosen from Welles and Cosgriff, 1965)

Specimen	A	B
	Approx.	*Approx.*
1. *Breadth of skull index:* B : Lx 100 ———	*81*	*75*
2. *Breadth of snout index:* S : Lx 100 As juveniles tend to have a relatively broader snout (Bystrow and Efremov, 1940), breadth is only significant when comparing skulls of a similar degree of maturity ———	*40*	*42*
3. *Height of skull index:* H : L x 100 A division could be made at about 16 and above (deep skulls), and below 16 as shallow skulls	*17,2*	*17,4*
4. *Interorbital breadth index:* A : Lx 100 The difference between the two indices is due to the excessive length of Specimen B—it must be remembered that severe distortion of this specimen in the snout area may have produced this difference ———	*16,1*	*8,8*
5. *Interotic breadth index:* C : Lx 100 ———	*27,1*	*19,5*
6. *Index of interorbital breadth relative to interotic breadth:* A : C × 100	*59,4*	*45,1*
7. *Orbit to otic notch: Interotic breadth index:* N : Cx 100	*59,4*	*61,2*
8. *Midline distance behind orbits of parietal foramen: Interotic breadth index:* P : Cx 100———	*16,5*	*9,6*
9 *Midline distance in front of otic notches of parietal foramen: Interotic breadth index:* T : Cx 100———	*33,1*	*38,7*
10. *Posterior skull border concavity index:* K : Cx 100 ———	*19,3*	*32,0*

Table 3

Comparison of Specimen A and B to type specimens of Parotosaurus pronus (Howie, 1969)

Characters	*Type Specimens*	*Specimen A*	*Specimen B*
Otic Notch	Semiclosed	Not known	Semiclosed
Tabular Horns	Expanded distally towards squamosal	Not known	Expanded distally towards squamosal
H : B x 100	23	17,2	17,4 (this figure was incorrectly printed as 20 in Chernin and Cruickshank, 1970)
Nares	Elongate, lateral, long axes parallel to skull border	Elongate, lateral, long axes parallel to skull border	Elongate, lateral, long axes almost parallel to skull border
Orbits	Close together well posterior oval, long axes parallel to midline	Close together well posterior, oval, long axes parallel to midline	Very close together posterior, oval, long axes almost parallel to midline
Pineal Foramen	Rectangular, just posterior to hind border of orbits	Shape unknown, just posterior to hind border of orbits	Rectangular, just posterior to hind border of orbits
Skull breadth B : L index	Skull broad posteriorly 75	Skull broad posteriorly 81	Skull broad posteriorly 75
Frontal and jugal enter orbital margin	Yes	Yes	Not known
Supratemporal excluded from otic notch	Yes	Yes	Not known
Snout breadth S : L index	Skull tapers anteriorly 32	Skull tapers anteriorly 40	Skull tapers anteriorly 42
Exoccipital barely exposed on palate	Yes	Yes	Yes
Pterygoid with facet for jaw articulation	Yes	Yes	Not known
Processus lamellosus of exoccipital present	Yes	Yes	Not known

Table 4

Stratigraphy

		South Africa	*Zambia*	*East Africa*
TRIASSIC	Upper	*Cave Sandstone* *Red Beds*		
	Middle	*Molteno*	Red Marls	Manda Formation
	Lower	*Cynognathus zone* *Lystrosaurus zone*	N'tawere Formation ?Escarpment Grits	?Kingori Sandstone

DISCUSSION

Briefly reviewing the four other species of *Parotosaurus* in which the tabular has grown laterally towards the squamosal, it is found that in *P. semiclausus* (Swinton, 1927) the tabular is unexpanded distally and only just fails to meet the squamosal. The orbits are more rounded and the jugal is excluded from the orbital margin. Although the tabular horn of *P. birdi* (Brown, 1933) and *P. peabodyi* (Welles and Cosgriff, 1965) have moved laterally, they still do not expand distally. Also *P. peabodyi* has a much shallower occiput and Howie (1969) has pointed out that the vertebrae of *P. peabodyi* differ from those of *P. pronus*. *P. birdi* has a greater exposure of exoccipital on the palate than *P. pronus* and the orbits are further apart in *P. birdi*.

P. brookvalensis (Watson, 1958) has a distal expansion of the tabular, but this is a bulbous swelling, which increases the surface area rather than causing it to approach the squamosal. Howie (1969) has discounted the proposal that *P. brookvalensis* is a juvenile of *P. pronus*, because of the character of its ornament and the length of the snout, which are both adult in proportion.

In the type specimen of *Parotosaurus pronus* (Howie, 1969), the tabular is expanded laterally towards the squamosal. Although this expansion is greater in the type specimen of *P. pronus* than in Specimen B, the significance lies not in the absolute size (Welles and Cosgriff, 1965), but in the distinct shape of the tabular horn, which in Specimen B is just about the only region not distorted or damaged, and corresponds to that region in the type species. The difference in the size of the distal expansion of the tabular and the whole skull could be due to genetic variability in populations.

The height to breadth ratio (H : B x 100) is 23 in the type specimen and 17,2 and 17,4 in Specimen A and B respectively. This difference is largely due to post-mortem deformation which also included dorso-ventral flattening, which is discussed more fully below.

The fact that in Specimen B the nares and orbits are not quite parallel to the skull border as they are in Specimen A and the type specimen is almost certainly due to post-mortem lateral compression.

Specimen B corresponds exactly to the type species with regard to the skull breadth index (B : L is 75). However, Specimen A has a greater skull breadth index (81). This is due, mostly, to the great difficulty in joining the small fragments in that area; small gaps remain between abutting fragments which, added together, caused this difference (see Fig. 1).

In the type species the snout breadth index (S : L) is 32. For Specimen A this value is 40, and for Specimen B 42. There seems no doubt that even taking into consideration the lack of the snout in Specimen A and the distortion of that area in Specimen B, the Luangwa Valley animals have broader snouts than the type specimen, which may be due to their larger size compared with the type.

I have had the opportunity of studying the almost complete skulls from the Ruhuhu Valley, now in the Cambridge Museum, and can confirm the triangular nature of their shape. With regard to Specimen B, the great expansion of the preorbital region makes the shape of the skull almost oval (without, of course, considering the quadrate region). This could mean that, with better material, new facts may emerge to cast doubt on the taxonomy and Specimen B could be a different species. With the available material this latter conclusion would presume too much.

With regard to Specimen A, however, the total lack of the snout and the difficulty involved in fitting the fragments together explain the difference in the snout index. As the indices were obtained from direct measurement, not taking into account the many small gaps, the morphological details (of the braincase (for example) convince me that Specimen A is most likely to be *Parotosaurus pronus*.

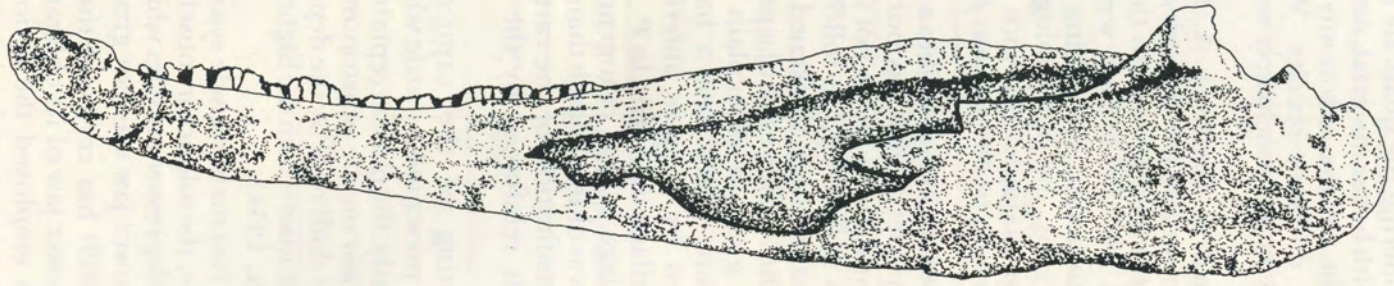
Howie (1969, p. 215) describes a pre-articular fossa in the type species, which has not been described in other labyrinthodonts and is not found in Specimen A. This fossa is described as follows: "The (hamate) process is transversely thickened and is excavated medially by the leading edge of a pre-articular fossa". Howie then goes on to explain that in the other labyrinthodonts which have a hamate process this fossa is filled by a more anterior ossification of Meckel's cartilage than seen in *P. pronus*. As ossification of cartilage is also ontogenetic, I suggest that Specimen A was older at death than the type specimen, and hence ossification of the cartilage filled in this fossa. This is reinforced by the larger size of the specimen.

The opening of the capitosaur mouth has traditionally presented a puzzle which former writers solved variously, the most acceptable being the resting of the lower jaw on the substratum together with the raising of the skull roof by the depressor mandibulae muscle, which inserted on the highest point of the skull roof (Watson, 1958).

There are two main muscle systems which support the lower jaw, the adductor muscles (which close the jaw) and the depressor muscles which would open the jaw—if the lower jaw was not grounded.

Howie (1969) has reviewed the problem and, in freeing the lower jaw of its obligation to hit the substratum, has employed the action of three muscle systems; the occipitovertebral muscle (which insert on the more or less vertical occiput and run to the cervical vertebrae); the cleidomastoideus muscle (which originates on the dorsal process of the clavicle and inserts on a projecting flange of the tabular) and the depressor muscle, which inserted along the cheek region of the occiput on the squamosal and quadratojugal—so that origin and insertion of the muscle are in the same vertical plane—the point of at-

FIG. 11 A.



11 B.

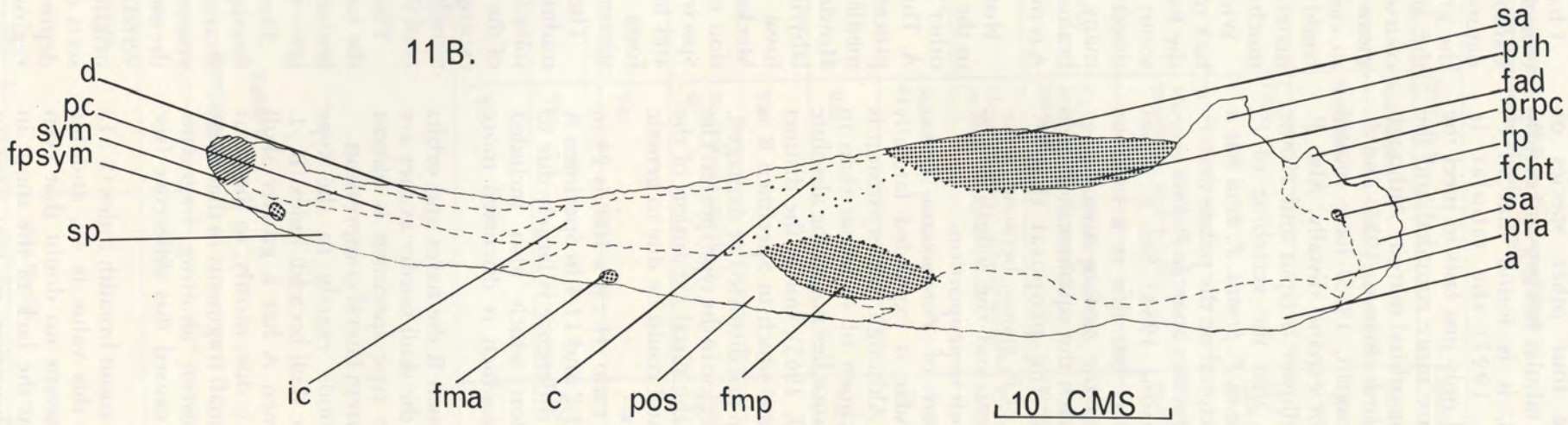


Fig. 11A. Lower jaw of Specimen A, seen lingually. (Reversed from left side)
Fig. 11B. Reconstruction and analysis of lower jaw of Specimen A, seen lingually.

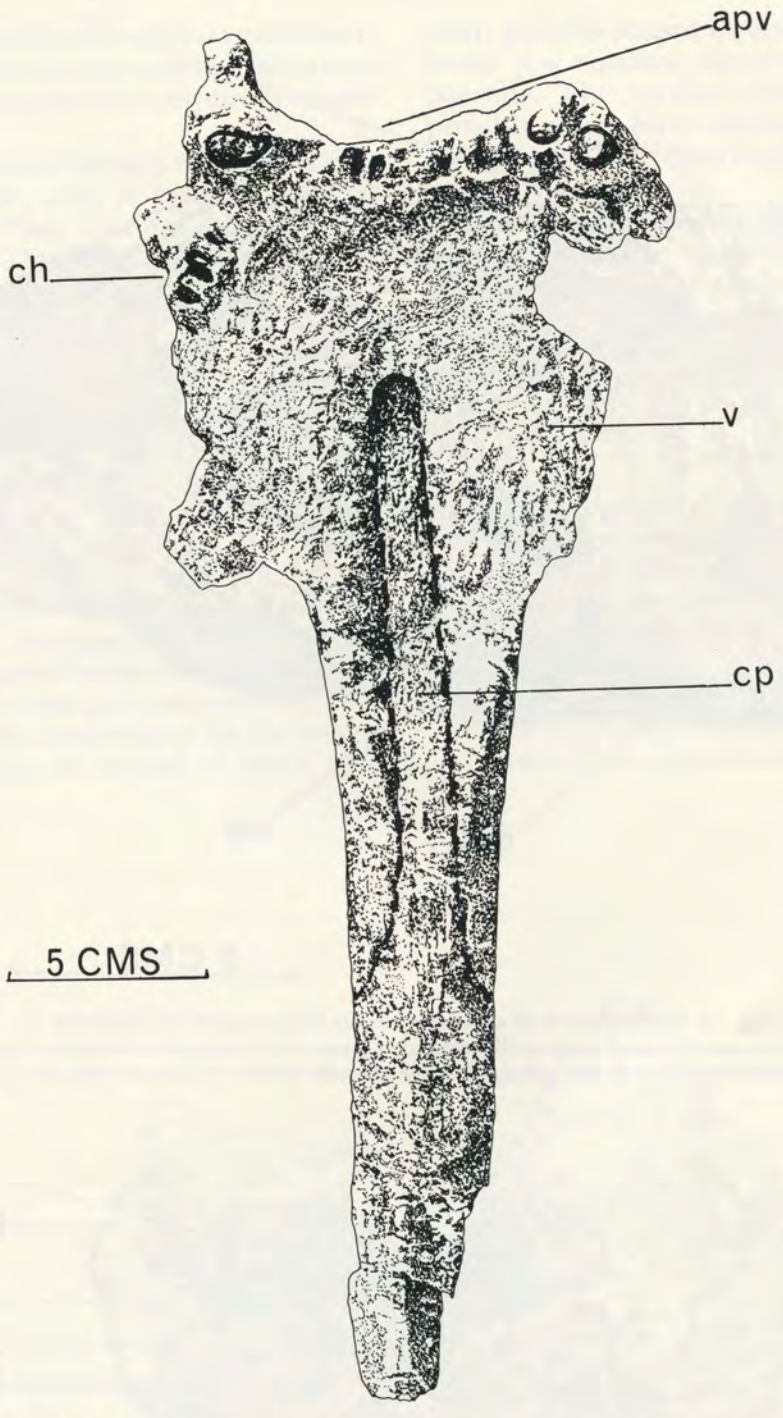


Fig. 12. Palatal view of vomer and clutriform process of Specimen A, as preserved.

tachment on the lower jaw being the slight medial inturning of the retroarticular process.

Howie's solution has two phases; firstly the skull is raised using the occipito-vertebral muscles and then the cleidomastoideus muscles, and secondly the jaw is lowered by the action of the depressor muscles.

I suggest another simpler mechanism. There is no doubt the capitosaurs were aquatic (the lateral line system and rete vasculosum found in capitosaurs are habitus characters of aquatic animals). If they did venture on land their progress would have been ponderously slow, leaving little doubt that they had little need to open their mouths on land with a view to catching prey. The position of their eyes (on the top of their heads and also centrally placed) makes it difficult to believe they could see, stalk, lie in wait and therefore catch a meal on land.

So, assuming the animals fed in water, on fish, which they could see, they must have been totally buoyant. The modern animal with an analogous way of life is the crocodile. On observation of these animals in glass tanks, it is clear that at no time is the jaw firmly closed. Whether resting, swimming or just walking on the bottom, there is a small gap between the jaws. This allows water to be continuously in the mouth, thus equalizing the pressures inside and outside the mouth;

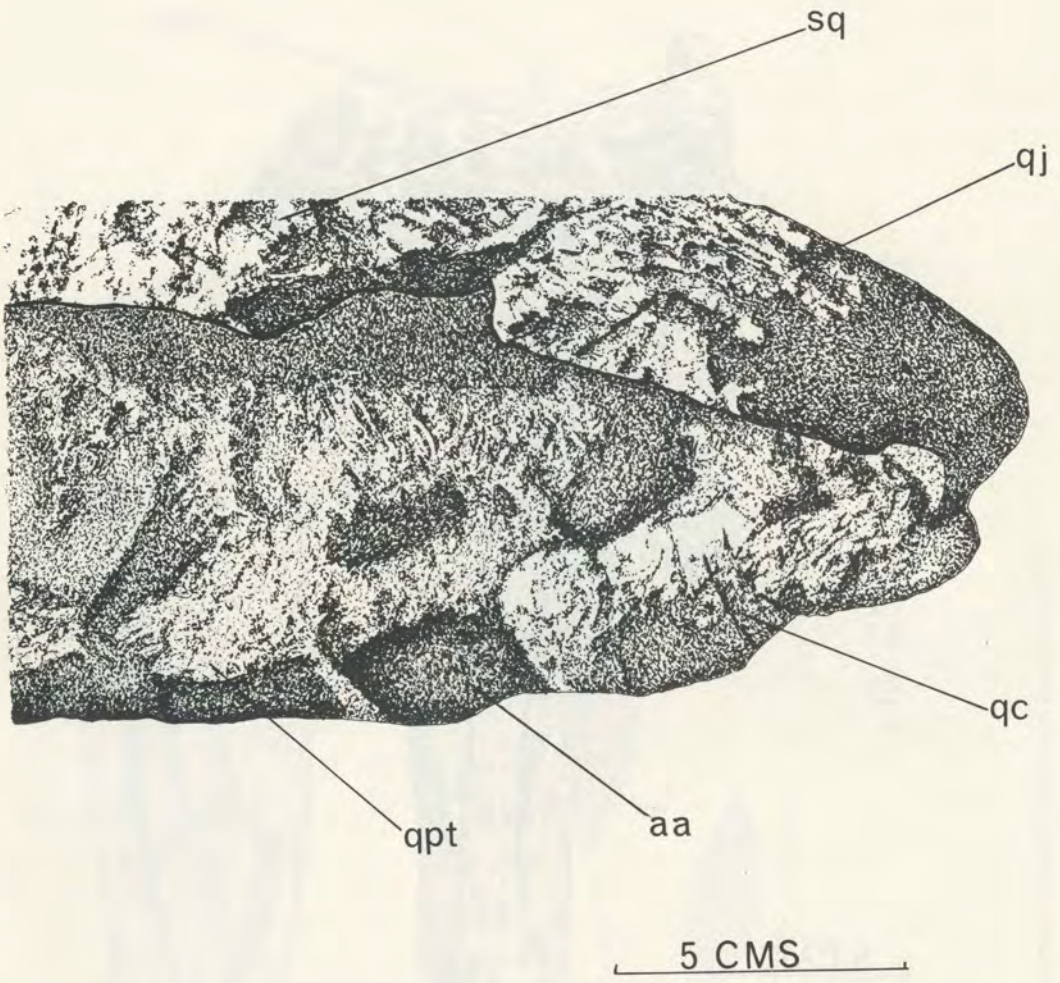


Fig. 13. Internal view of quadrate ramus of pterygoid of Specimen A.
N.B. A distinction of *P. pronus* is a roughened area of bone on the quadrate ramus of the pterygoid in an internal position adjacent to the quadrate. This appears to have been a continuation on to the pterygoid of the articular surface of the screw-shaped quadrate condyle. (Howie, 1969)

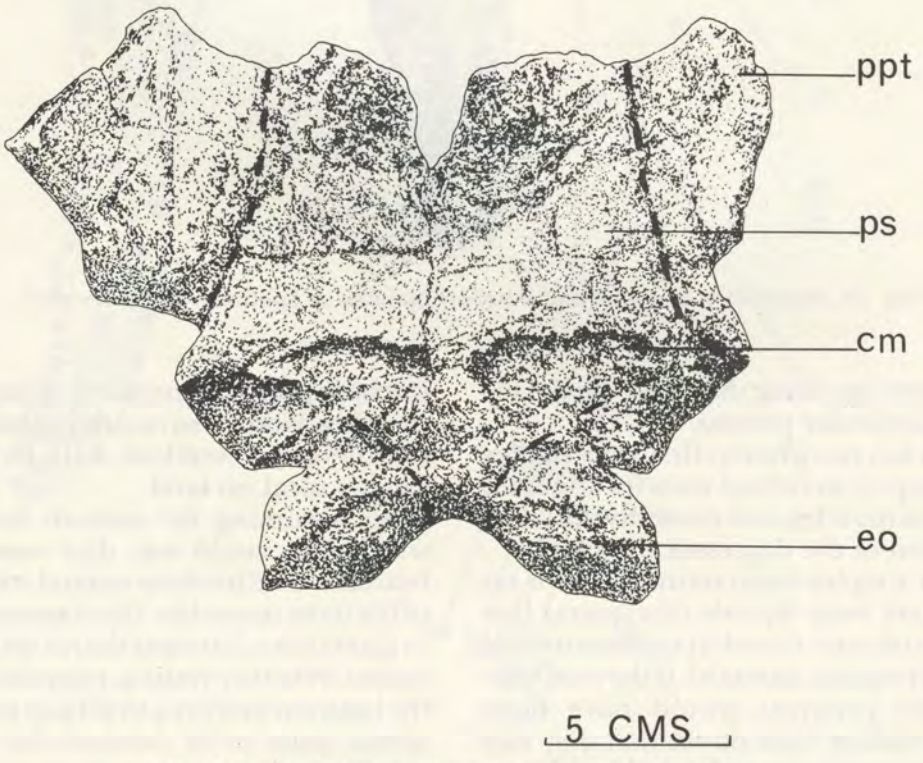


Fig. 14. Ventral view of occipital region of Specimen A.

then when it wants to open the mouth less resistance is applied by the water acting against a partial vacuum in the mouth, thus decreasing the force required to open the mouth.

A second interesting point emerged while observing crocodiles; whenever they snap at prey the jaw first opens a distance away from the prey and then the animal lurches forward. This means that the inrush of water completes the widening of the gape without great muscular exertion.

The opening of the capitosaur jaw by lowering of the jaw instead of raising the skull roof would also enable the animal to keep sight of its prey.

Assuming that capitosaurs preyed in a similar fashion to the crocodile, if there was a depressor mandibularis muscle originating on the tabular horn flange and inserting on the roughened area of the retroarticular process, (Watson, 1958), this would mean that, when the muscle was contracted, a force would be exerted which, resolved into vectors, would have a vertical and horizontal component, the latter of which would tend to move the jaw rami medially. This latter force is adequately counteracted by the screw-shaped quadrate condyle, the thread of which runs from postero-lateral to antero-medial directions. A lower jaw rotating about this condyle must move laterally. The vertical component of the force is possibly all the force necessary to open the jaw in the conditions I have described, with the animal floating neutrally buoyant.

Thus, to summarize, it is necessary to employ only one muscle system to open the mouth of capitosaurs, the depressor mandibular muscles, with the assumption that the capitosaurs fed in a similar fashion to the modern crocodile.

SUMMARY

1. Capitosaur material collected from the fossiliferous beds of the N'tawere Formation in the Upper Luangwa Valley, Zambia is described.
2. These are tentatively assigned to the genus and species *Parotosaurus pronus* Howie, on the basis of the similarity in proportions as well as other details (Specimen A), and the diagnostic otic notch, in which the tabular has expanded laterally towards the squamosal (Specimen B).

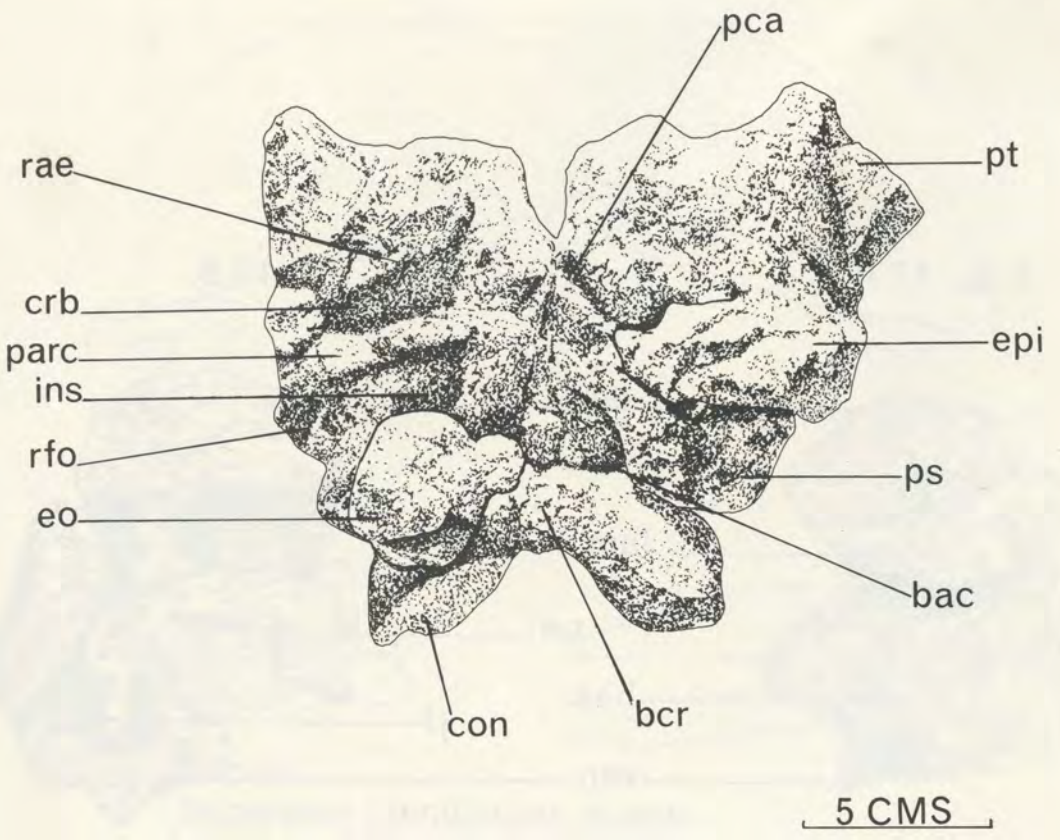


Fig. 15. Dorsal view of Braincase of Specimen A.
N.B. The right exoccipital is missing.

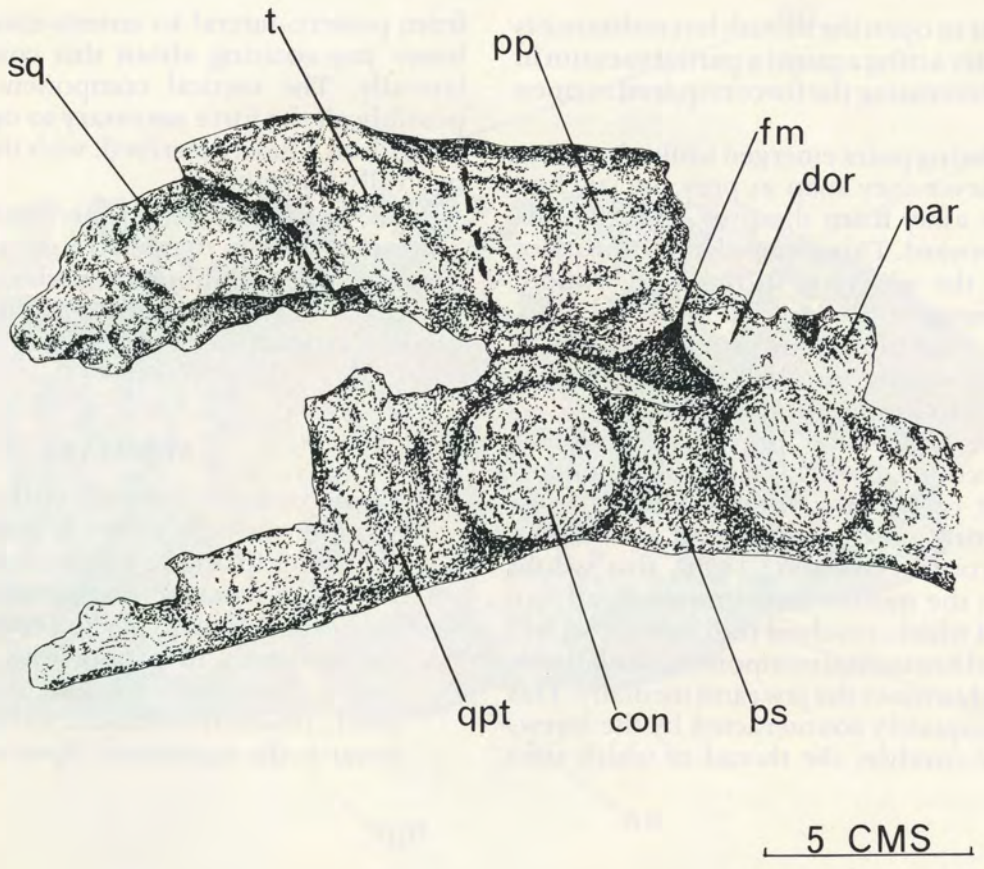


Fig. 16. Posterior view of occipital view of Specimen B.

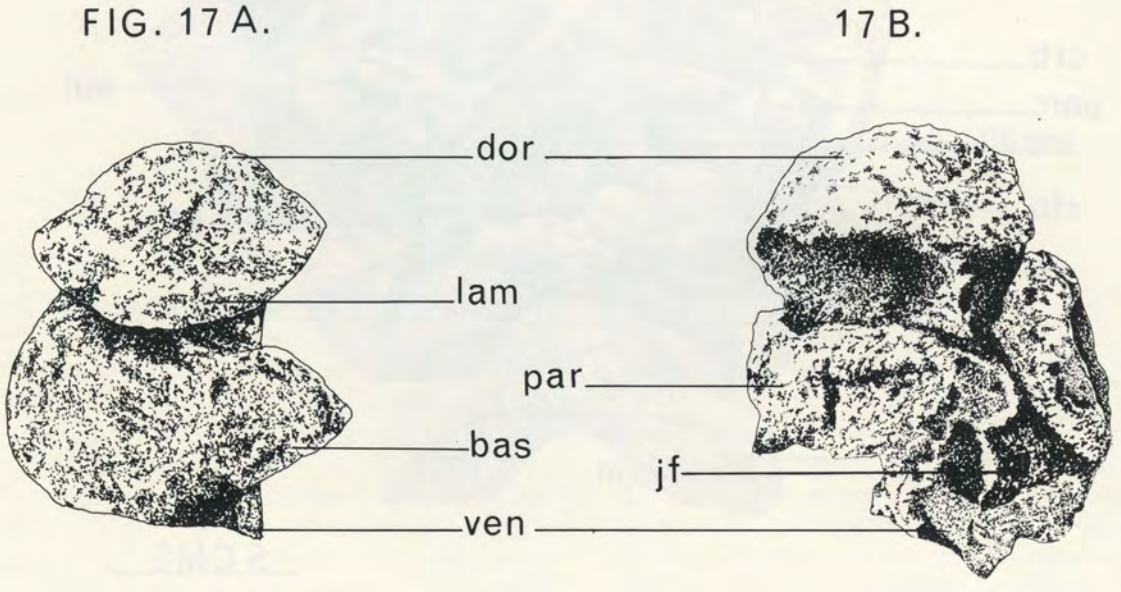


Fig. 17A. Median view of left exoccipital of Specimen A.
Fig. 17B. Lateral view of left exoccipital of Specimen A.

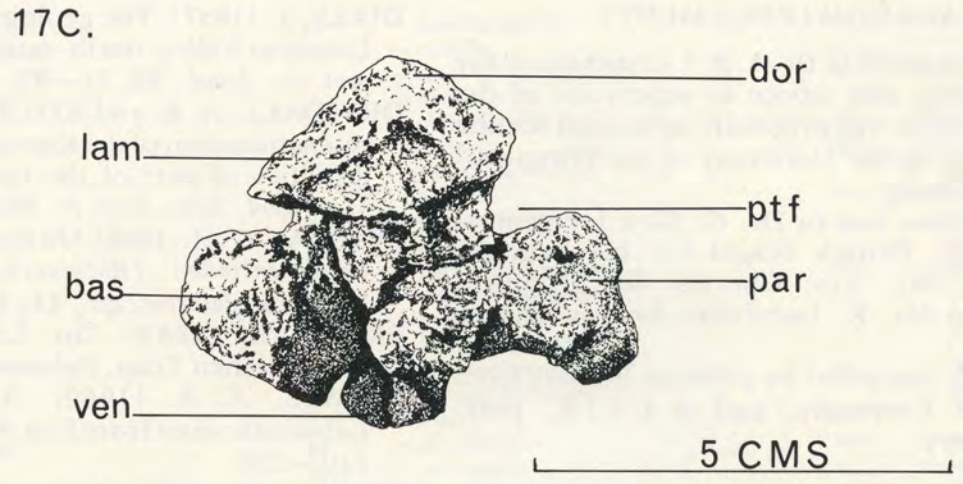


Fig. 17C. Anterior view of left exoccipital of Specimen A.

3. The only other *Parotosaurus pronus* from another locality, described to date, is that described by Howie (1969), which was collected from Mkongoleko, Ruhuhu Valley, Tanzania, in the Manda Formation.
4. Points 1, 2 and 3 corroborate evidence put forward by Dixey (1937), Crompton (1955), Crompton and Ellenberger (1957) and Drysdall and Kitching (1969) that the N'tawere Formation in the Upper Luangwa Valley and the Manda Beds represent the same horizon.
5. A consideration of faunal units of the relevant horizons and on the assumption that the foregoing is correct leads to the conclusion that the "Red Marl" horizon of N'tawere is largely equivalent to that of the Mkongoleko area of the Manda Formation and that both of these post-date the *Cynognathus* zone only slightly. The lower of the two N'tawere horizons may, in fact, be of the same age as the *Cynognathus* zone.
6. Assuming capitosaurs had a similar life-style to the modern crocodile, and the animals were neutrally buoyant, it is suggested that only the depressor mandibulae muscles were necessary to open the mouth, by lowering the lower jaw.

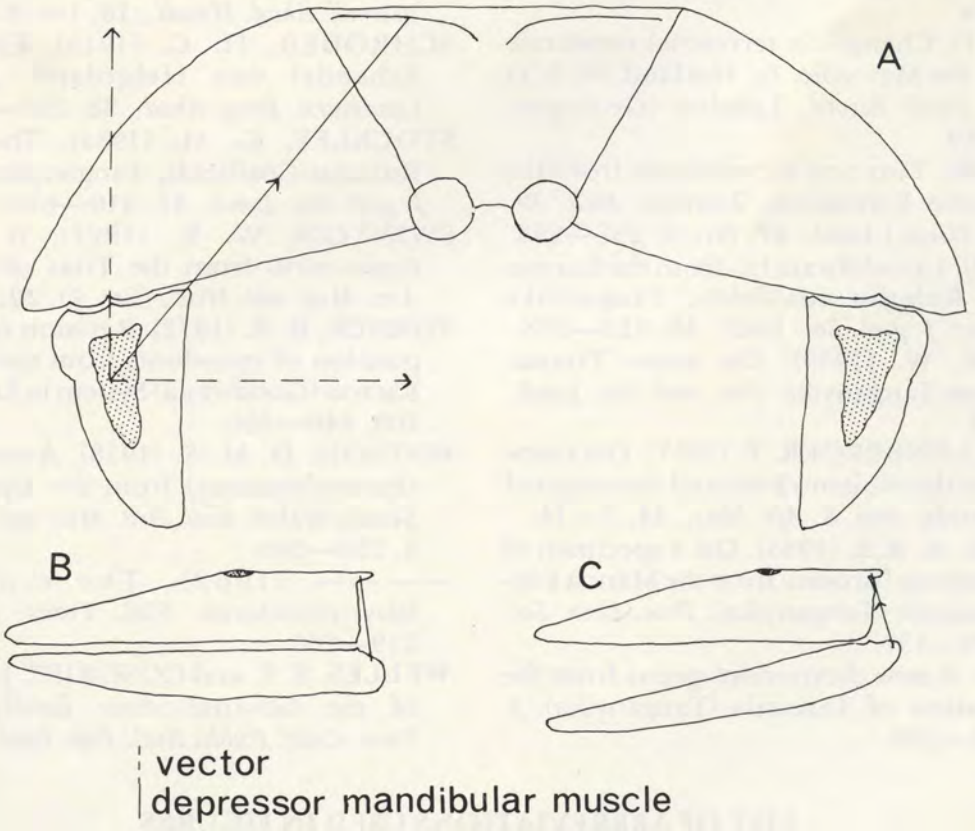


Fig. 18. Semi-diagrammatic representation of a suggested mechanism for opening the mouth in capitosaurs, if the animals are neutrally bouyant.

A. Posterior view of skull and jaw, showing line of action of force exerted by the depressor mandibular muscle. This force is also shown resolved into its vertical and horizontal vectors.
B. Lateral view of relaxed skull and jaw, showing position of depressor mandibular muscle.
C. Lateral view of skull with jaw lowered, showing line of action of depressor mandibular muscle when contracted.

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LIST OF ABBREVIATIONS USED IN FIGURES

a — angular
aa — auxiliary articulatory area
ac — anterior commisure
apv — anterior palatine vacuity
art — articular
bac — basioccipital chamber
bas — basal process
bcr — barioccipital crest
c — coronoid

ch — choana
cm — crista muscularis
con — condyle
cp — cultriform process
crb — conical recess for the basipterygoid process
d — dentary
dor — dorsal process
ec — ectopterygoid
eo — exoccipital
epi — epipterygoid
f — frontal
fad — adductor fossa
fcht — chorda tympani foramen
fm — foramen magnum
fma — anterior Meckelian foramen
fmp — posterior Mekelian foramen
fogl — glenoid fossa
fpsym — postsymphysial foramen
ic — intercoronoid
inl — infraorbital canal
ins — intercrestal sulcus
iv — interpterygoid vacuity
j — jugal
jf — jugular foramen
jl — jugal canal
la — lacrimal
lam — lamellar process
mx — maxilla
n — nasal
nr — nare
obr — oblique ridge
p — parietal
paf — paraquadrate foramen
pafn — parietal foramen
pal — palatine
par — paroccipital process
parc — parapterygoid crest
pc — precoronoid
pca — internal opening of palatine branch of the internal carotid artery
pf — postfrontal
pmx — premaxilla
por — postorbital
pos — postsplenial
pp — postparietal
ppt — palatine ramus of pterygoid
pra — prearticular
pref — premaxillary foramen
prf — prefrontal
prh — hamate process of prearticular
prprc — precondylar process
prptc — postcondylar process
ps — parasphenoid
pt — pterygoid
ptf — post-temporal fossa
q — quadrate
qc — screw-shaped quadrate
qj — quadratojugal
qpt — quadrate ramus of pterygoid
rae — roughened area for the attachment of the epipterygoid
rfo — ridge marking fenestra ovalis in the dorsal groove of the pterygoid
rp — retroarticular process
sa — surangular
sacc — sulcus accessorius
sf — subtemporal fenestra
smand — sulcus mandibularis
soral — sulcus oralis
sp — splenial
sq — squamosal
st — stapes
stp — supratemporal
sul — supraorbital canal
sym — symphysis
t — tabular
tl — temporal canal
tr — trough for depressor mandibular muscle
v — vomer
ven — ventral process

Palaeont. afr., **17**, 57—68 1974

EVOLUTIONARY TRENDS IN TRIASSIC DICYNODONTIA

(Reptilia Therapsida)

by

A. W. Keyser

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ABSTRACT

Triassic Dicynodontia differ from most of their Permian ancestors in a number of specialisations that reach extremes in the Upper Triassic. These are (1) increase in total body size, (2) increase in the relative length of the snout and secondary palate by backward growth of the premaxilla, (3) reduction in the length of the fenestra medio-palatinalis combined with posterior migration out of the choanal depression, (4) shortening and dorsal expansion of the intertemporal region, (5) fusion of elements in the front part of the brain-case, (6) posterior migration of the reflected lamina of the mandible, (7) disappearance of the quadrate foramen and the development of a process of the quadrate that extends along the quadrate ramus of the pterygoid. It is thought that the occurrence of the last feature in *Dinodontosaurus platygnathus* Cox and *Jacheleria colorata* Bonaparte warrants the transfer of the species *platygnathus* to the genus *Jacheleria* and the erection of a new subfamily, Jachelerinae nov.

It is concluded that the specialisations of the Triassic forms can be attributed to adaptation to a *Dicroidium*-dominated flora.

INTRODUCTION

The Anomodontia were the numerically dominant terrestrial herbivores during the transition between Palaeozoic and Mesozoic time. They achieved their greatest diversity during the Upper Permian as is clear from the abundance of forms that are encountered in the Lower stage of the Beaufort Series of the Karroo System of South Africa and other Upper Permian strata in Africa including the Madumabisa Mudstone of Zambia and those in the Ruhuhu area of Tanzania.

Most of the Permian species of Dicynodontia were relatively small, but giant forms developed at times. Upper Permian reptilian faunas are uncommon on most of the continents and are only known from areas in Africa, India, U.S.S.R., Scotland and possibly China. As far as is known most of the Indian species are relatively small (Kutty, 1972). During the Triassic most of the Dicynodontia were large and show a number of peculiar specialisations not commonly encountered in Permian forms. These specialisations form the subject matter of this paper.

Evolutionary trends in Dicynodontia were first described by Toerien (1953 and 1955). He pointed out that the most significant trend along which Anomodontia developed was the tendency to increase the extent of the secondary palate with concomitant increase in the relative size of the palatine bones and a reduction in the size of the ectopterygoid and of the inter-pterygoid vacuity.

Cox (1965) pointed out that there is a tendency for an increase in size in the Triassic Dicynodontia which he divided into three families. He drew particular attention to shortening of the intertemporal region in the Triassic forms.

Cruickshank (1967) elaborated on many of the advanced features mentioned by Cox (1965) and added several new features to the list of known distinguishing features between Permian and Triassic Dicynodontia. In 1968 he also wrote a short paper in which the quantitative aspects of the increase in the relative size of the interpterygoid vacuity with the passage of geological time is discussed.

The evolutionary trends envisaged by these authors and a few other trends that can be noticed will be briefly discussed in the following pages.

(a) *Increase in total Body Size.*

Although most of the Permian forms are relatively small, giant forms occasionally developed in Lower Beaufort time. Most of the species known from the *Tapinocephalus* Zone of the Lower Beaufort Stage are relatively small with skull lengths very seldom more than 10 cm. During the following *Cistecephalus* Zone time numerous giant forms developed e.g. *Endothiodon, Aulacephalodon* and *Rhachiocephalus*. Skulls of the latter often reached a length of 50 cm and more (Keyser 1969, 1971).

During *Daptocephalus* Zone times several large Dicynodonts such as *Daptocephalus* and *Dinanomodon* replaced the large *Cistecephalus* Zone forms.

Most of the known Triassic dicynodont genera had skulls that were longer than 20 cm in adult specimens, the only exceptions being:

1. *Myosaurus gracilis* from the (Lower Triassic) *Lystrosaurus* Zone of South Africa.
2. A small dicynodont with a narrow intertemporal region discovered in the *Cynognathus* Zone (Lower Triassic) near Burgersdorp in the Republic of South Africa. The specimen is being described by Dr. N. Hotton III of the Smithsonian Institution.
3. Two species of smaller dicynodonts from the Puesto Viejo Formation of Argentina are currently being described by Dr. J. Bonaparte of the Instituto Miguel Lillo of Tucuman, Argentina. One of these, *Vinceria andina,* has been briefly described and figured (Bonaparte, 1971).
4. *Jimusaria* is a small dicynodont that does not appear to be a juvenile of one of the larger Chinese species. The age of this form is possibly Permian.

Some of the largest known species of dicynodonts lived during the Triassic. *Ischigualastia* from the Ischigualasto Formation of Argentina, *Placerias* from the Chinle Formation of Arizona and *Stahleckeria* from the Santa Maria Beds of Brazil are the largest forms in the group. All these genera are Upper Triassic in age. The youngest known dicynodont from the Carnian (uppermost Triassic) Los Colorados Formation of Argentina *Jacheleria colorata* Bonaparte 1971, though large, is smaller than these three genera.

(b) *Increase in the relative length of the Snout and Secondary Palate.*

When illustrations of Triassic dicynodonts are compared with similar illustrations of Permian forms one is immediately struck by the long snouts displayed by the Triassic genera (see Fig. 1). The degree of importance of long snouts is intensified by the relative shortness of the intertemporal regions of the Triassic species.

In the Middle Beaufort genus *Lystrosaurus* the snout is lengthened in a ventral direction (Cluver, 1971). The tendency to develop a long snout is only shown by *Kannemeyeria* among the lower Triassic genera. *Myosaurus* and the new form being described by Hotton from South Africa, the Chinese *Shansiodon,* and *Vinceria andina* from South America exhibit more or less the proportions of Permian dicynodonts.

During the Anisian the trend towards very long snouts is apparent. *Tetragonias njalilus* and *Rhopalorhinus etionensis* do not have very long snouts. *Kannemeyeria* was still in existence. The species of *Rechnisaurus* from India and the N'tawere Formation of Zambia are apparently very similar to *Kannemeyeria.* This genus has been placed in the family Stahlekeridae of Cox (1965) by both Chowdury (1970) and Crozier (1970). The specimens do, however, have a prominent ridge on the dorsal surface of the premaxilla and are both deformed so that there can be no certainty about the crested nature of the intertemporal region. In the author's opinion this genus had best be placed in the family Kannemeyeridae and is probably a descendant of the genus *Kannemeyeria.* It is even doubtful that a generic distinction can be upheld.

The members of the genus *Dolichuranus* from South West Africa and the N'tawere formation of Zambia (Keyser, 1973 b) have longer snouts than are found in *Tetragonias* and in this as well as in other respects approach the Upper Triassic *Dinodontosaurus* from South America.

All the known Upper Triassic dicynodont genera have exceedingly long snouts when compared with Permian, Lower and Middle Triassic forms. Examination of Fig. 29 of the paper by Cox (1965) emphasizes this statement (see also Fig. 1 in this paper). Extremes in this trend are the Chinese *Sinokannemeyeria* and *Parakannemeyeria* as well as the South American *Ischigualastia* and *Dinodontosaurus.*

Concomitant with the elongation of the snout there is an increase in the length of the secondary palate. A trend towards the increase of the length of the secondary palate was first described by Toerien (1953). At the time when Toerien wrote his paper most of the Triassic dicynodonts were still unknown. The later Triassic forms with extremely long snouts like *Dinodontosaurus* and *Ischigualastia* show this increase in the length of the secondary palate to an extreme and can therefore be regarded as the most advanced dicynodonts (Fig. 2).

Toerien demonstrated the existence of a trend to increase the extent of the secondary palate by an increase in size and forward growth of the palatine bones. This mainly applies to Permian genera. The most advanced forms, showing the most extensive palatine participation in the secondary palate, are *Tropidostoma,* an endothiodont, *Aulacephalodon, Pelanomodon, Oudenodon* and *Rhachiocephalus.* These are all advanced Permian forms.

In many of the Triassic genera the palatines are insignificant in the secondary palate, most of which is made up by the premaxillae, e.g. *Dinodontosaurus.* In these forms the very extensive secondary palate is due to backward growth of the premaxilla.

This is in part achieved by the exclusion of much of the maxilla from the roof of the mouth. This type of palatal structure is already found in the Upper Permian genus *Daptocephalus* (Ewer, 1961). In this genus the premaxilla has a posterior outgrowth that meets the palatines. The posterior outgrowth is much broader in the Lower Triassic genus *Kannemeyeria.* In many of the Upper Triassic forms e.g. *Dinodontosaurus* the palatine bones are no longer very extensive. (Fig. 2.)

(c) *Trend towards reduction of the interpterygoid vacuity.*

The relationships of the secondary palate and the interpterygoid vacuity have also been discussed by Cruickshank (1968). He showed quantitatively that

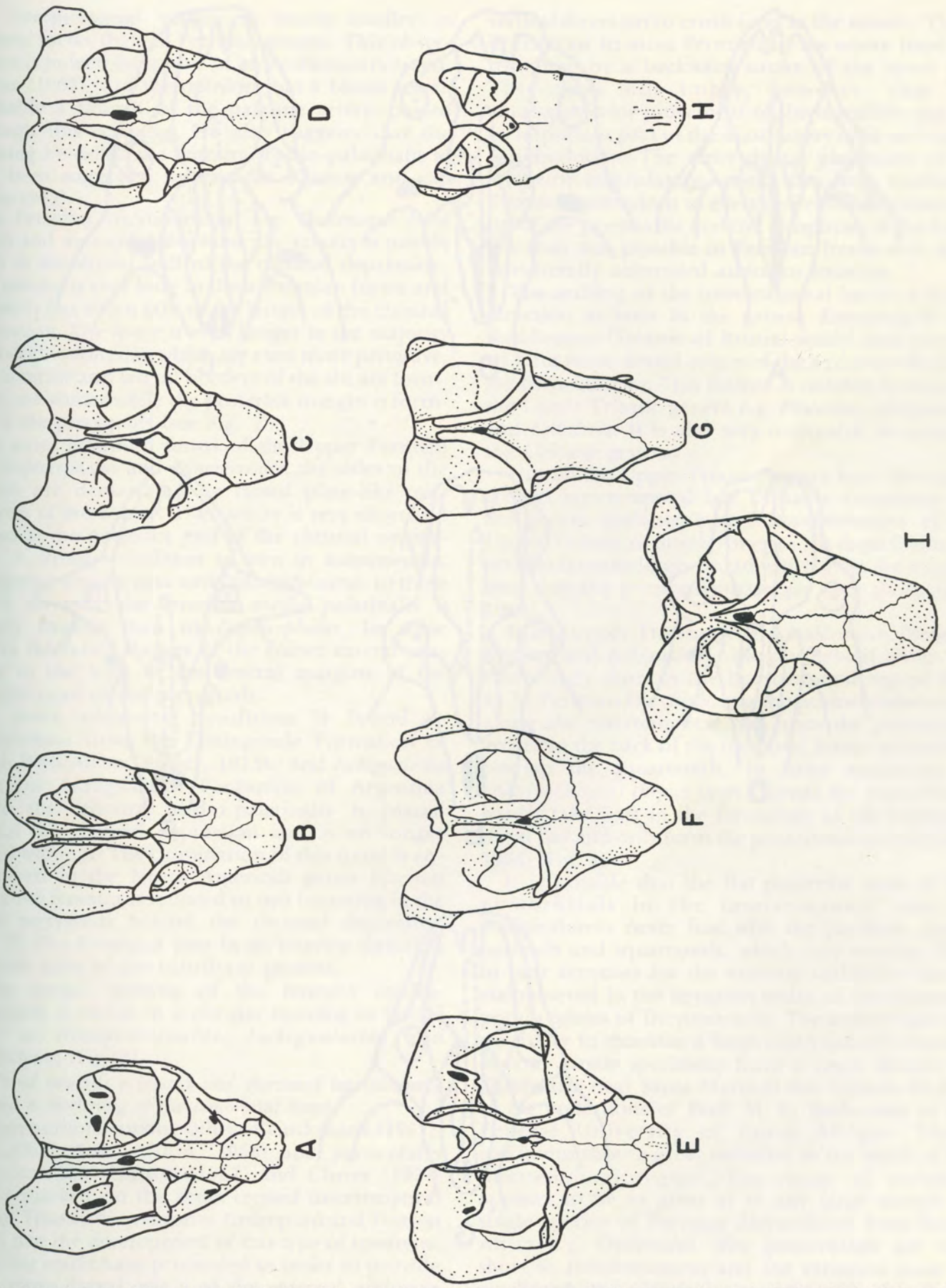

Fig. 1. Dorsal views of Permian and Triassic Dicynodontia (reduced to the same size for comparison). A, *Oudenodon baini* Owen (Permian); B, *Daptocephalus leoniceps* (Owen) (Permian); C, *Tetragonias njalilus* (Von Huene) (Triassic); D, *Ischigualastia jenseni* Cox (Triassic); E, *Aulacephalodon baini* (Owen) (Permian); F, *Kannemeyeria simocephala* (Weithofer) (Triassic); G, *Dolichuranus primaevus* Keyser (Triassic); H, *Parakannemeyeria dolichocephala* Sun Ai Lin (Triassic); I, *Dinodontosaurus platyceps* (Cox) (Triassic). Modified after various authors.

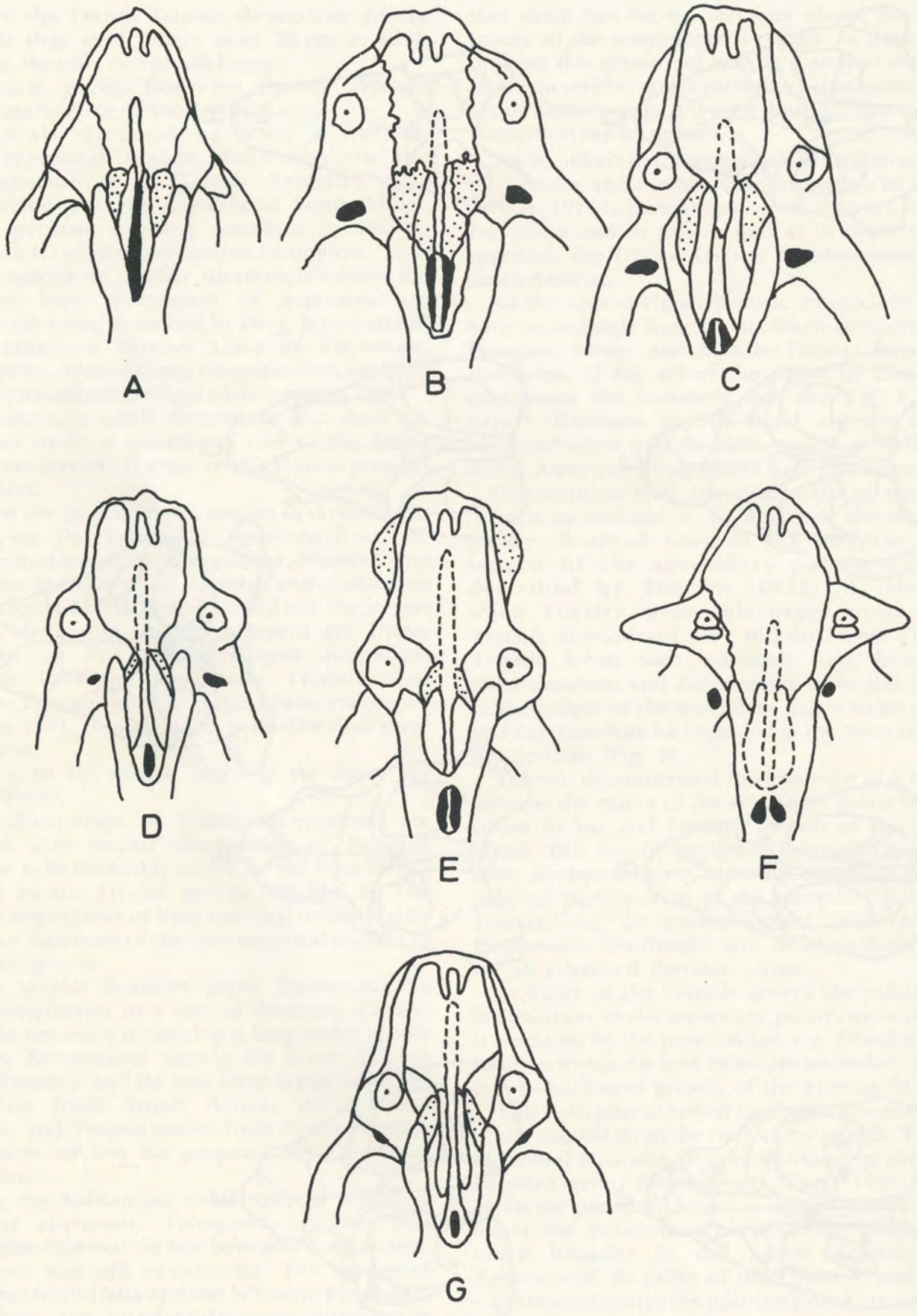

Fig. 2. Palatal view of Permian and Triassic Dicynodontia to show the development of the secondary palate and the interpterygoid vacuity. (all reduced to the same size). Palatine bones are indicated by dotting. A, *Oudenodon baini* Owen (Permian); B, *Aulacephalodon baini* (Owen) (Permian); C, *Daptocephalus leoniceps* (Owen) (Permian; D, *Kannemeyeria simocephla* (Weithofer) (Triassic); E, *Rhopalorhinus etionensis* Keyser (Triassic); F, *Placerias gigas* Camp and Wells (Triassic); G, *Dinodontosaurus platyceps* (Cox).

the interpterygoid vacuity is much smaller in Triassic forms than in Permian genera. This observation is indeed indicative of an evolutionary trend.

Cox (1968) is of the opinion that a blood vessel, probably a branch of the palatine artery, passed through this opening. He also suggests that the opening be called the fenestra medio-palatinalis as had been suggested by van der Klaauw and van Roon(1942).

In Permian Dicynodontia, e.g. *Oudenodon baini* Owen and *Aulacephalodon baini,* the vacuity is merely a slit in the dorsal wall of the choanal depression. The vacuity is very long in these Permian forms and normally has about 60% of the length of the choanal depression. The space is even longer in the majority of Endothiodontidae which are even more primitive. The anterior and lateral borders of the slit are formed by the vomer while the posterior margin is formed by the pterygoids (see Fig. 2).

In more advanced forms of the Upper Permian e.g. *Daptocephalus* and *Dinanomodon* the sides of the vacuity are demarcated by raised plate-like outgrowths of the vomer. The vacuity is very short and placed at the posterior end of the choanal depression. A similar condition is seen in *Kannemeyeria, Tetragonias, Dolichuranus* and *Dinodontosaurus.* In these forms however the fenestra medio-palatinalis is slightly smaller than in *Daptocephalus.* In these genera the raised flanges of the vomer extend ventrally to the level of the ventral margins of the palatine rami of the pterygoids.

A more advanced condition is found in *Rhopalorhinus* from the Omingonde Formation of South West Africa (Keyser, 1973b) and *Ischigualastia* from the Ischigualasto Formation of Argentina where the fenestra medio-palatinalis is placed behind the choanal depression and is no longer placed within it. The culmination of this trend is encountered in the North American genus *Placerias* where the fenestra is reduced to two foramina in the fused pterygoids behind the choanal depression (Fig. 2). The foramina pass in an interior direction on both sides of the cultriform process.

The dorsal opening of the fenestra medio-palatinalis is visible as a circular opening in lateral view in *Dinodontosaurus, Ischigualastia* and *Dolichuranus* (Fig. 3).

(d) *Trend towards a crested and shortened intertemporal bar and a shortening of the postorbital bones.*

Many authors, among others Cruickshank (1967), Cox (1965), Sun, Ai-Lin (1963) and particularly Crompton and Hotton (1967) and Cluver (1971) have remarked on the short crested intertemporal bars of Triassic dicynodonts. Crompton and Hotton noted that the development of this type of intertemporal bar could have proceeded in order to provide for a more dorsal origin of the external adductor musculature.

This more dorsal placement of the main muscles associated with the masticatory mechanism would have enabled the animals to exert more force in a vertical direction to crush food in the mouth. This is in contrast to most Permian forms where food was triturated by a backward stroke of the lower jaw. This does not imply, however, that the anteroposterior movement of the mandible was not an important part of the masticatory cycle of Triassic Anomodontia. The more dorsal placement of the adductor musculature would also have enabled a Triassic anomodont to exert more force between the tip of the premaxilla and the symphysis of the lower jaw than was possible in Permian forms with more horizontally orientated adductor muscles.

The arching of the intertemporal bar in a dorsal direction as seen in the genera *Kannemeyeria* and *Rabidosaurus* (Triassic of Russia) would have provided for a more dorsal origin of the adductor externus medialis muscles. This feature is notable in many of the Upper Triassic genera e.g. *Placerias, Ischigualastia* and *Jacheleria.* It is also very noticeable in many of the Chinese genera.

Not all the Upper Triassic genera have the raised crested intertemporal bar. Notable exceptions are the genera *Stahleckeria* and *Dinodontosaurus* of the Upper Triassic of South America. In these forms the occiput is exceedingly broad which gives the impression that the temporal fossae are very short (Cox, 1965).

In the Upper Triassic genera *Stahleckeria, Dinodontosaurus* and *Ischigualastia* the postorbital bones are exceedingly short in the intertemporal region (Fig. 4). In Permian Dicynodontia the postorbitals extend along the intertemporal bar from the postorbital arches to the back of the temporal fossae where they overlap the squamosals. In some specimens of *Dinodontosaurus turpior* (von Huene) the postorbitals hardly take part in the formation of the intertemporal bar and only form the postorbital arches (Cox, 1968) (Fig. 4).

It is notable that the flat posterior rami of the postorbitals in the intertemporal bars of Anomodontia never fuse with the parietals, interparietals and squamosals, which they overlap. This in part accounts for the extreme variability that is encountered in the apparent width of the intertemporal regions of Dicynodontia. The author had opportunity to examine a large collection of *Dinodontosaurus turpior* specimens from a single locality at Candelaria near Santa Maria in Rio Grande do Sul, in the collections of Prof. M. C. Barbarena of the Federal University of Porto Allegre. These specimens show a great variation in the width of the intertemporal region. The range of variation appears to be as great as in any large sample of single species of Permian dicynodonts from South Africa e.g. *Oudenodon.* The postorbitals are very short in *Dinodontosaurus* and the variation must be attributed to ontogenic variation in the living animals.

In the Indian genus *Wadiasaurus* Roy Chowdury from the Yerapalli Formation and in *Sangusaurus* Cox from the N'tawere Formation of Zambia,

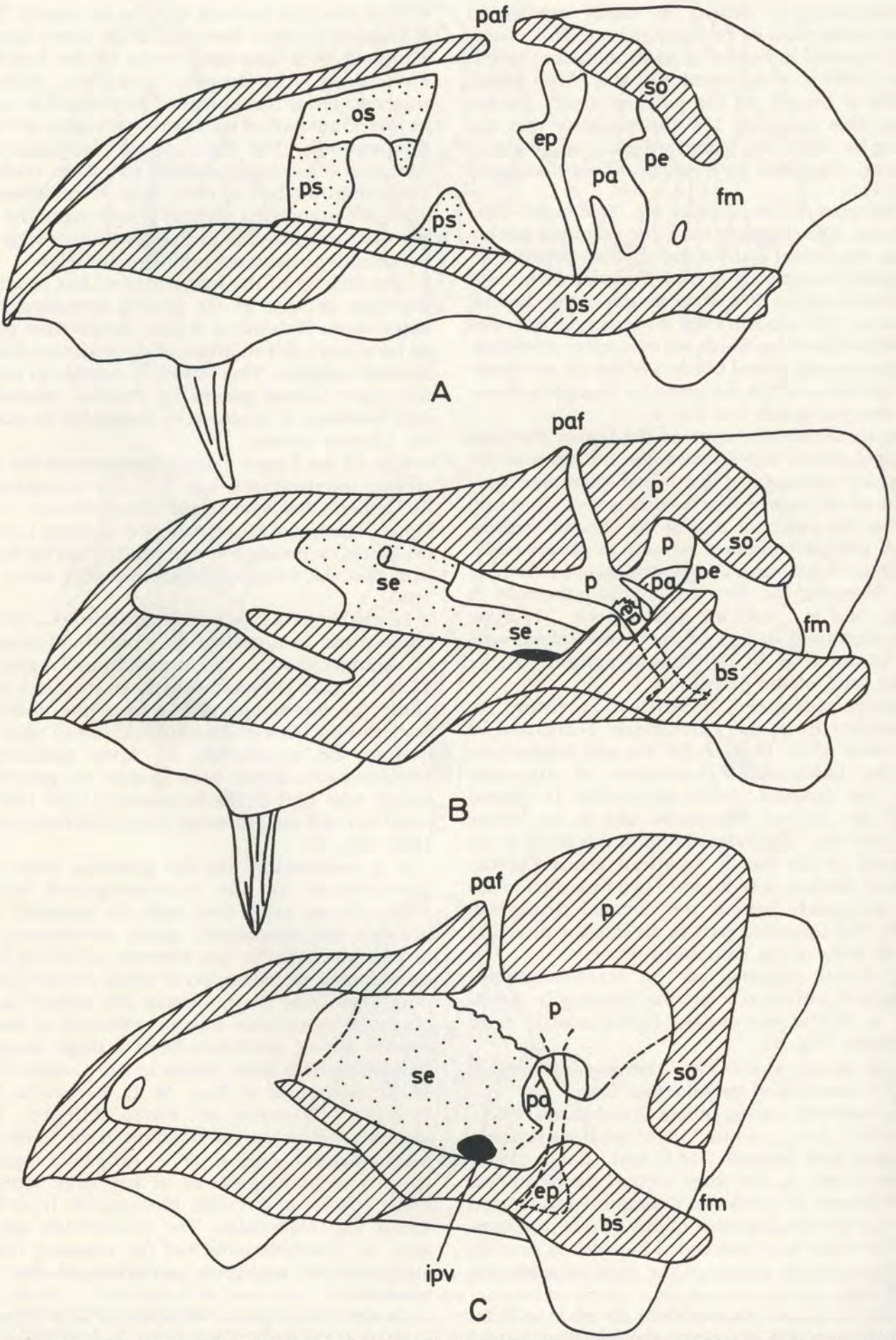

Fig. 3. Schematic reconstruction of saggital views to show the evolution of the sphenethmoid region in Dicynodontia (all reduced to the same size). A, *Dicynodon grimbeeki* Broom (after Agnew) (Permian); B, *Aulacephalodon baini* (Owen) (Permian); C, *Ischigualastia jenoseni* Cox (Triassic). The sphenethmoid is indicated by dotting. Cross hatching indicates the plane of section. Abbreviations: bs, basisphenoid, ep, epipterygoid, fm, foramen magnum, ipv, interpterygoid vacuity, os, orbitosphenoid, p. parietal, pa, pila antotica, paf, parietal foramen, pe, periotic, ps, presphenoid, se, sphenethmoid (undifferentiated,) so, supraoccipital.

peculiar boss-like thickenings of the postorbitals occur on the intertemporal region behind the level of the parietal foramen. There can be no certainty about the function of these bosses but it is conceivable that they could have related to sexual dimorphism as is found in living African Suidae where bosses occur on the maxillae of both sexes but are very large in sexually active males.

(e) *Fusion of elements in the Brain-case.*

In Permian Dicynodontia the back part of the brain-case is enclosed by the various occipital elements and the basis cranii. Farther forward the sides of the brain-case are formed by the periotics. The prootic and opisthotic are indistinguishably fused in most Dicynodontia. In anomodonts the sides of the front part of the brain are normally quite open and have no bony covering. In this open area the sides of the brain received some limited support from the finger-like processes of the prootic commonly referred to as the pila antotica and also the epipterygoids. Anterior to this the optical and olfactory lobes of the brain were probably housed in the orbitosphenoid wings of the sphenethmoid complex.

In most Permian Dicynodontia the sphenethmoid region consists of an anterior orbitosphenoid ossification formed of a vertical plate that stands in a groove on the dorsal surface of the cultriform process. This plate divides dorsally into two wing-like plates that probably contained the olfactory and optical lobes. A more posterior element normally referred to as the presphenoid also stands in the groove on the dorsal surface of the cultriform process. This condition is found in *Dicynodon grimbeeki* Broom (Agnew, 1958), *Pristerodon buffaloensis* Toerien (Barry, 1967) and *Cistecephalus microrhinus* Owen (Keyser, 1973a).

In more advanced Permian genera like *Oudenodon, Rachiocephalus* and *Aulacephalodon* (Keyser, in press) the anterior sphenethmoid ossification fuses with the posterior presphenoid element to form a single sphenethmoid ossification.

In many Triassic species the sphenethmoid fuses with the two ventral plates that the parietals send down to meet the epipterygoids and possibly even with the prootic. The only part of the brain that is laterally exposed in these forms is a small fenestra formed lateral to the sella turcica in the region of the prootic incisures for the passage of the nervus trigeminus.

This condition can be clearly seen in *Kannemeyeria* and in a specimen of *Ischigualastia* that belongs to the Instituto Lillo in Tucuman (Fig. 3).

It is interesting to note that fusion between the sphenethmoid and the parietals and prootics also occurred in moschopid Dinocephalia of the very much earlier *Tapinocephalus* zone of probably Middle Permian age (Boonstra, 1968).

(f) *Specialization of the Suspensorium and Lower Jaw.*

In Permian Dicynodontia as well as in most Triassic genera of Anomodontia the quadrate consists of a main condylar part, the lateral side of which is fused to the quadratojugal which in turn fuses with the squamosal and a median dorsal process. The dorsal process of the quadrate is firmly clamped between the paroccipital process of the periotic and the squamosal. Because of the fusion with quadratojugal very little or no movement of the quadrate relative to the rest of the skull was possible.

In the genera *Daptocephalus, Kannemeyeria, Dolichuranus, Tetragonias, Vinceria* and *Dinodontosaurus* the arrangement of the quadrate and quadratojugal is exactly as is found in the Permian genera.

The holotype of *Dinodontosaurus platygnathus* Cox 1968 from the Ischichuca Formation of Argentina exhibits an odd specialization of the quadrate not encountered in other anomodonts. (Figs. 5 and 6).* The anterior face of the dorsal process of the quadrate has a long tapered anterior process that lies along the outside of the quadrate process of the pterygoid for nearly its whole length. The dorsal process of the quadrate is reduced and is much smaller than that of Permian Dicynodontia. Examination of a large number of specimens of *Dinodontosaurus turpior* and *Dinodontosaurus platyceps* in South American collections have clearly shown that no pterygoid process is ever developed in these two species. It is therefore necessary to remove the species *platygnathus* from the genus *Dinodontosaurus.*

The quadrate foramen which is normally a slit-like opening between the quadrate and the quadratojugal is circular in *Dinodontosaurus platygnathus* and is placed close to and nearly above the condylar part of the quadrate.

The only dicynodont in which the quadrate foramen is absent is the South American genus *Ischigualastia* (Fig. 7). Concomitant with the disappearance of the quadrate foramen the reflected lamina of the lower jaw is placed very far back on the ramus and forms a posterior process on the ventral side of the ramus that touches the anteroventrally directed tip of the retroarticular process of the articular (Fig. 7).

The quadratojugal is a vertically placed plate of bone that extends from the lateral condyle of the quadrate to the lateral occipital flange of the squamosal in all other known dicynodonts. This plate is always nearly parallel to the long axis of the skull. In *Ischigualastia* the flat quadratojugal is not orientated parallel to the long axis of the skull but is swung out laterally to be orientated at nearly 90° to the long axis of the skull. This results in the disappearance of the quadrate foramen. It can be said that the foramen opens up to such an extent that it disappears.

As a generalisation it can be said that the quadrate foramen is generally wider and shorter in Triassic Dicynodontia than in Permian forms.

In Permian Dicynodontia the posterior edge of the reflected lamina of the angular is placed at about

* The type specimen of *Platycyclops crassus* Broom 1948 also displays this feature.

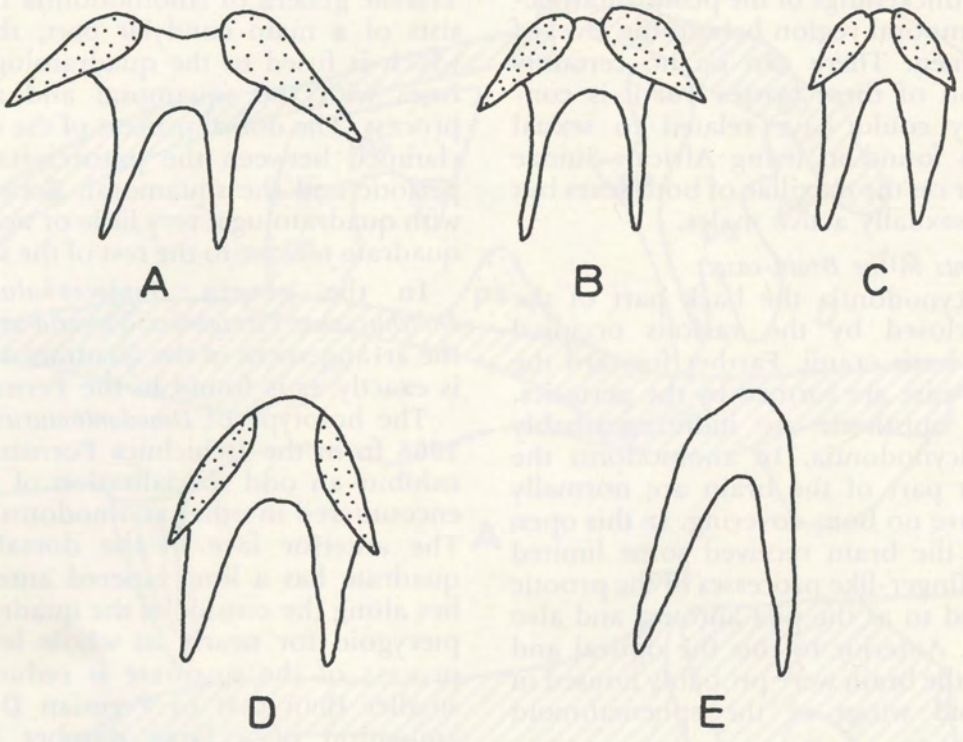

Fig. 4. Sections through the intertemporal regions of various Permian and Triassic Dicynodontia, immediately posterior to the parietal foramen. All reduced to the same size. Postorbital bones are indicated by dotting. A, *Rhachiocephalus,* B, *Daptocephalus,* C, *Dolichuranus,* D, *Kannemeyeria,* E, *Dinodontosaurus.*

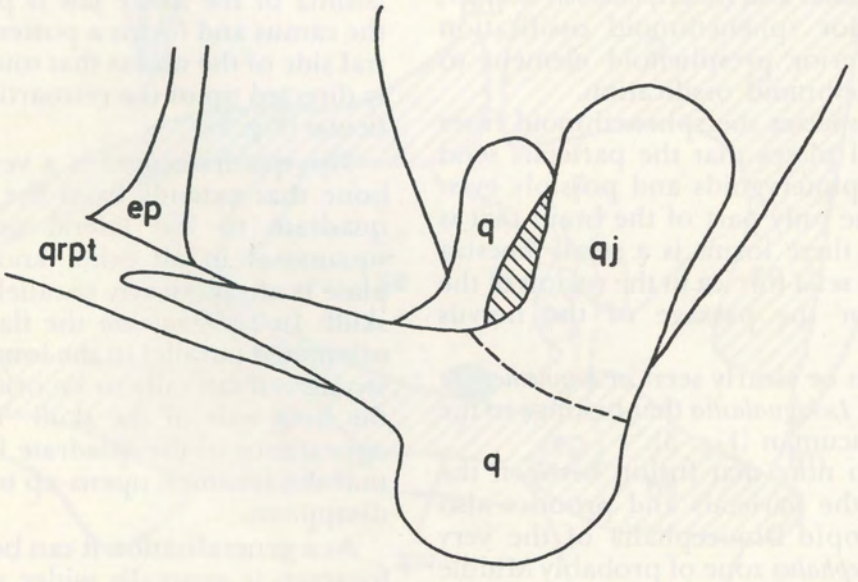

Fig. 5. Lateral view of the quadrate region of *Jacheleria platyceps* (about $\frac{1}{3}$ natural size). Abbreviations: ep, epipterygoid, q, quadrate, qj, quadratojugal, qrpt, quadrate ramus of pterygoid.

the level of the posterior third of the length of the ramus of the lower jaw.

In most Triassic Dicynodontia the reflected lamina is placed farther back and nearer to the articular. This is particularly noticeable in the *Rechnisaurus* lower jaw described by Crozier (1970) and in the jaw of *Jacheleria platygnathus* (Cox). In all Triassic Dicynodontia the reflected lamina is nearer to the articular than is the case in *Oudenodon, Rhachiocephalus, Aulacephalodon, Pristerodon, Emydops* or *Cistecephalus*. The culmination of this trend is seen in *Ischigualastia* where the reflected lamina is in contact with the retroarticular process of the articular (Fig. 7).

It is clear that a broadening of the quadrate foramen is associated with posterior migration of the reflected lamina. The culmination of this trend is found in *Ischigualastia* where the reflected lamina meets the articular and where the quadrate foramen disappears. This indicates that there was a functional association between these two structures in Anomodontia.

DISCUSSION

The following trends and their culmination in various Triassic Dicynodontia are discussed:

a. Increase in total body size.
b. Increase in the relative length of the snout and secondary palate by backward growth of the premaxilla.
c. Reduction in the length of the fenestra mediopalatinalis and its posterior migration out of the choanal depression.
d. Shortening and dorsal expansion of the intertemporal bar with concomitant shortening of the temporal fossae.
e. Fusion of elements in the front part of the brain-case.
f. Posterior migration of the lamina reflecta of the mandible.
g. Development of an anterior process on the quadrate which lies along the quadrate ramus of the pterygoid.
h. Disappearance of the quadrate foramen.

The South American genus *Ischigualastia* from the Ischigualasto Formation of Argentina is morphologically the most advanced form of the Suborder Anomodontia and displays all the advanced features mentioned in this discussion except the pterygoid process of the quadrate.

All these specializations can be attributed to adaptation of the masticatory mechanism to changes in environment including the food supply that was available to the animals. It is well known that a total change of the flora of the Southern Hemisphere occurred at the base of the Triassic when the *Glossopteris* flora was replaced by a *Dicroidium* flora dominated by pteridosperms and Bennettitales on all the Gondwana continents. The diet of Permian Dicynodontia probably consisted mainly of equisetalians and *Glossopteris* (Keyser, 1971) while the Triassic forms had to rely on the very different *Dicroidium* flora. It is therefore possible to relate the specializations of the masticatory apparatus to adaptation to the *Dicroidium* flora.

The genus *Daptocephalus* from the Uppermost Permian of the Beaufort Series of South Africa shows many of the advanced features of the later Triassic genera. Among these the long snout and secondary palate formed largely by backward growth of the premaxilla, the tiny posteriorly placed interpterygoid vacuity, the narrow intertemporal crest and short temporal fossae may be mentioned. These specializations indicate that *Daptocephalus* could be ancestral to many of the Triassic genera. It is also notable that *Daptocephalus* lived at a time when the *Glossopteris* flora was about to be superseded by a different flora. The evolutionary position of *Daptocephalus* will be discussed in a subsequent paper.

The evaluation of the advanced features encountered in the Triassic Dicynodontia leads to the consideration of their taxonomic significance.

The types of both *Jacheleria colorata* Bonaparte and *Dinodontosaurus platygnathus* Cox are very poor and fragmentary specimens. The type of *Jacheleria colorata* consists of a lower jaw and a very weathered posterior two-thirds of a skull. The type of *platygnathus* consists of a palate, an occiput and a lower jaw. The lower jaws of both species have a very flat profile along the dorsal surface and very long symphysial parts. Both species also have pterygoid processes on their quadrates. Although very little is known about these two species and though they are not of the same age it is best to refer the species *platygnathus* Cox to the genus *Jacheleria* Bonaparte. The development of a pterygoid process of the quadrate in both these species and the fact that such a process is not found in any other group suggests their removal from the Subfamily Stahleckeroinae (Lehman) and the erection of a new Subfamily *Jachelerinae* (nov.).

Cox (1968) described a new genus and species *Chanaria platyceps* from the Chanares Formation (now Ischishuca Bonaparte 1971) of Argentina which also contains specimens of *Dinodontosaurus brevirostris* Cox 1968. The former genus and species differs from the latter mainly in the extreme width of the intertemporal region of *Chanaria platyceps*.

In the light of the variation encountered in the Candelaria series of skulls the generic name *Chanaria* Cox must be regarded as a junior synonym of *Dinodontosaurus* Romer. As the species *platyceps* has page priority over *Dinodontosaurus brevirostris* the species found in the Ischichuca Formation has to be referred to as *Dinodontosaurus platyceps* (Cox).

Although there is not as wide a range of variation in the Triassic Anomodontia as is encountered in Permian forms (e.g. the difference between the giant *Rhachiocephalus* and smaller forms like *Cistecephalus* and *Emydops)* there is still enough variation to separate

the Triassic forms into several Subfamilies. The extreme forms of the Upper Triassic in which the various evolutionary lineages culminated are very different from one another but appear to be linked together by many intermediate genera and species. The large number of new discoveries that have been made in Africa, U.S.S.R., China and South America since 1965 when C. B. Cox proposed a classification of the Triassic dicynodonts into three families now indicate that major rethinking on the taxonomy of the group has become necessary.

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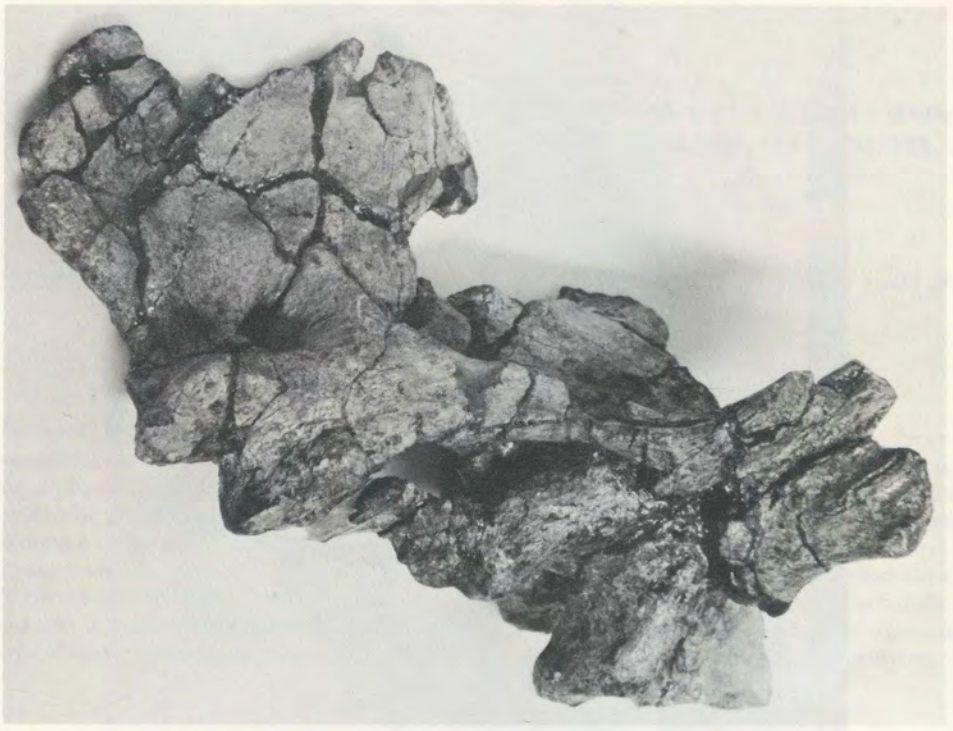

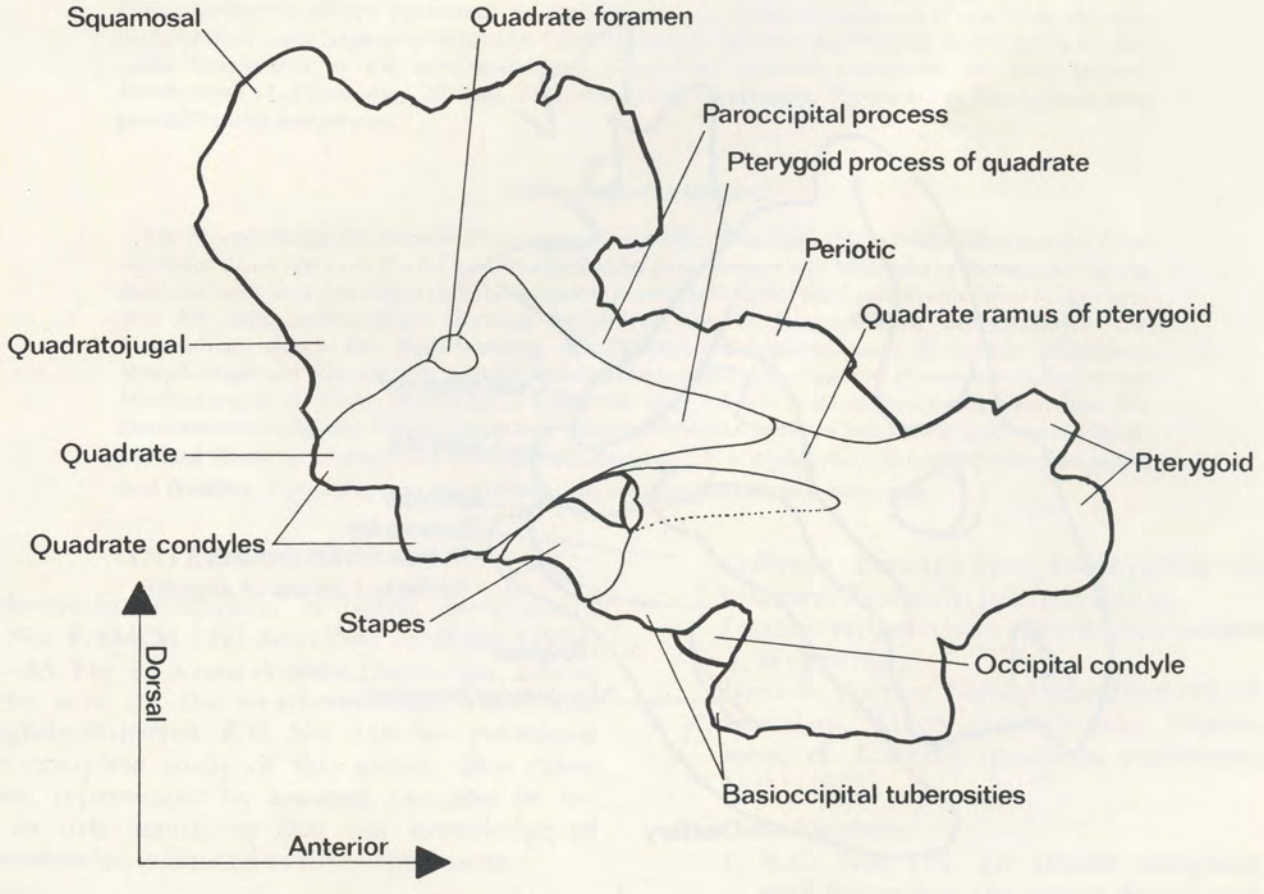

Fig. 6 *Upper*
Ventro-lateral view of the occipital part of the skull of *Jacheleria platyceps* showing the pterygoid process of the quadrate.
Lower
Tracing of photograph with the various elements annotated.



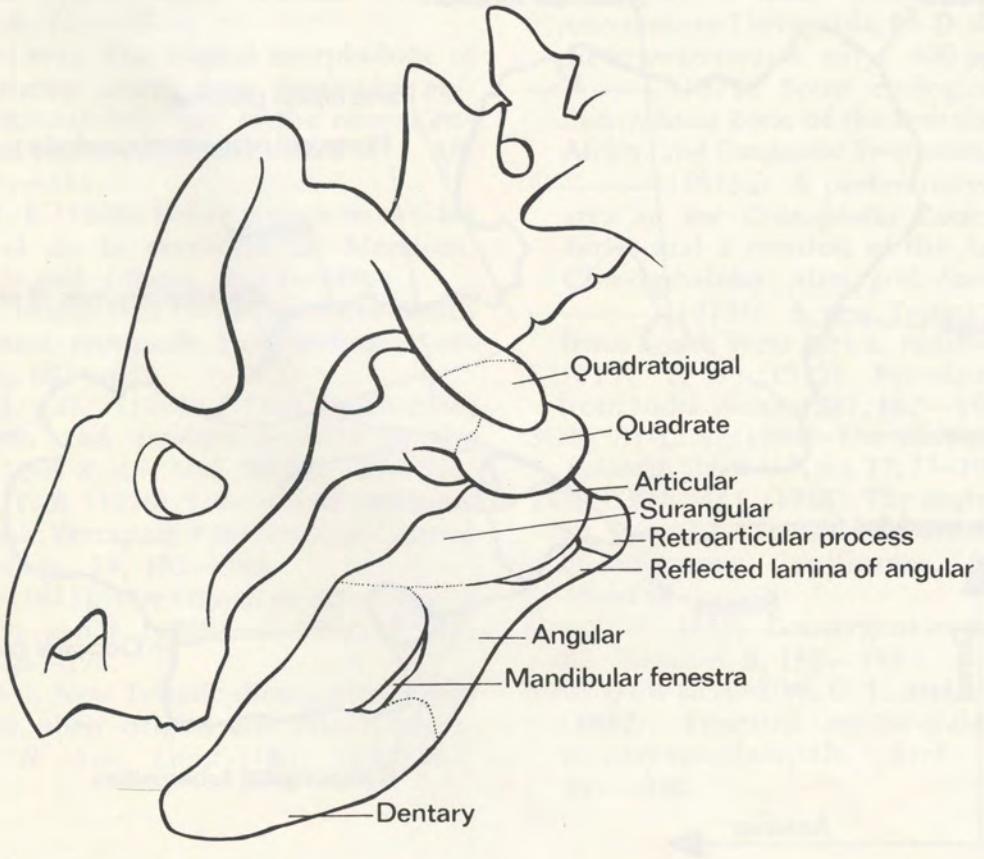

Fig. 7 *Upper*
Lateral view of the skull of a specimen of *Ischigualastia jenseni* in the museum of the Instituts Lillo, Tucumán, showing the joined reflected lamina and retroarticular process of the lower jaw and the absence of the quadrate foramen.
Lower
Tracing of photograph with the various elements annotated.

Palaeont. afr., **17**, 69—85 1974

A NEW SPECIMEN OF *PROMOSCHORHYNCHUS PLATYRHINUS* BRINK 1954 (MOSCHORHINIDAE) FROM THE *DAPTOCEPHALUS*-ZONE (UPPER PERMIAN) OF SOUTH AFRICA

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ABSTRACT

The morphology of the skull of *Promoschorhynchus platyrhinus* (Moschorhinidae) from the *Daptocephalus*-zone (Upper Permian) of South Africa) is described with special reference to the palate and posterior part of the skull. *Promoschorhynchus* is compared with *Moschorhinus* and considered to be a vaild genus mainly differing from *Moschorhinus* in retaining a longer snout, and in possessing a more primitive morphology of the palatal plates of the premaxillae and vomers.

Promoschorhynchus also differs from *Moschorhinus* in having developed a sharp *crista choanalis* and a fairly broad epipterygoid. The composition of the South African Moschorhinidae is briefly discussed and is considered temporarily as consisting of five genera: *Moschorhinus (? = Tigrisuchus). Cerdops, Promoschorhynchus* and *Hewittia. Tigrisuchus* and *Moschorhinus* are probably synonyms.

RÉSUMÉ

La morphologie du crâne de *Promoschorhynchus platyrhinus* (Moschorhinidae de la zone à *Daptocephalus* (Permien supérieur) d'Afrique du Sud) est étudiée en insistant sur la description du palais et de l'arrière crâne. *Promoschorhynchus* est comparé à *Moschorhinus* et considéré comme un genre valable différant essentiellement de *Moschorhinus* par la retention d'un plus long museau et d' une morphologie plus primitive des plaques palatales des premaxillaires et vomers. *Promoschorhynchus* diffère également de *Moschorhinus* par le développement d'une *crista choanalis* aiguë et d'un assez large épiptérygoide. La composition des Moschorhinidae sudafricains est discutée brièvement et est temporairement considérée comme constituée de cinq genres: *Moschorhinus (?=Tigrisuchus), Cerdops, Promoschorhynchus* et *Hewittia. Tigrisuchus* et *Moschorhinus* sont probablement synonymes.

ZUSAMMENFASSUNG

Die Morphologie des Schädels von *Promoschorhynchus platyrhinus* (Moschorhinidae aus der *Daptocephalus* Zone (Oberes Perm) von Südafrika) ist beschrieben mit besonderer Berücksichtigung des Gaumens und des hinteren Schädelteiles. *Promoschorhynchus* wird mit *Moschorhinus* verglichen, und für eine selbständige Gattung befunden. Sie ist hauptsächlich unterschieden von *Moschorhinus* durch die Beibehattung der längeren Schnautze, und der mehr primitiven Morphologie der Gaumenplatten der Prämaxillaren und der vomeren. *Promoschorhynchus* ist von *Moschorhinus* auch darin unterschieden dass sie eine scharfe *crista choanalis* entwickelt hat. Die Zusammensetzung der südafrikanischen Moschorhinidae ist kurz behandelt und vorläufig als aus funf Gattungen bestehend erachtet: *Moschorhinus, (? = Tigrisuchus), Cerdops, Promoschorhynchus* und *Hewittia. Tigrisuchus* und *Moschorhinus* sin sehr wahrscheinlich synonym.

INTRODUCTION

Promoschorhynchus platyrhinus is based on a snout (B.P.I. No. F.484/M.192) described by Brink (1954, pp. 43—45, Fig. 2). A new skull and lower jaw, almost complete, save for the weathered skull roof, and only slightly distorted (R.C. No. 116) has permitted a more complete study of this genus. One other specimen, represented by a snout, can also be included in this genus, so that our knowledge of *Promoschorhynchus* is limited to three specimens.

I *Material:*

A. *Holotype:* B.P.I. No. F.484/M.192: a snout including part of the interorbital region, but lacking the orbital margins; the lower jaw is missing.
Collection: Bernard Price Institute for Palaeontological Research, Johannesburg.
Locality: Wilgerbosch, New Bethesda (collector: J. W. Kitching).
Horizon: Former *Cistecephalus* zone (*s.l.*) (Upper Permian). More precisely the *Daptocephalus* zone, cf. Kitching (personal communication, 13/11/1973).

B. *Other Specimens:*

1. R.C. No. 116: an almost complete skull with lower jaw; the entire dorsal surface of the skull and dorso-lateral portions of the occiput have been weathered away.
Collection: Rubidge collection, Wellwood, Graaff-Reinet.

Locality: Wellwood, Graaff-Reinet (collector: Hans Wessels).
Horizon: Daptocephalus zone.

2. G.S.P., K.C. No. R.85: a snout, which on the basis of external characters (the palate is not completely available) can be regarded as representing a probable *Promoschorhynchus*.
Collection: Geological Survey, Pretoria, Keyser collection.
Locality: Ferndale, Graaff-Reinet (collector: André Keyser).
Horizon: Cistecephalus zone (*s.l.*), more precisely the *Daptocephalus* zone, cf. Keyser (personal communication, 21/11/1973).

II *Diagnosis:*

Promoschorhynchus is a moschorhinid which can be distinguished from *Moschorhinus* by the following features: (1) a more slender snout, more elongated in both the precanine and postcanine areas; (2) the nasals constricted at mid-length; (3) a broader epipterygoid with a posterior apophysis more ventrally located; (4) a clearer distinction between the mastoid and the quadrate processes of the opisthotic which are separated by a deep groove; (5) a premaxilla more widely expanded on the palate, especially at the mid-ventral line; (6) a less pronounced anterior expansion of the vomer both in length and breadth; (7) a sharp *crista choanalis,* which passes anteriorly to the upper canines and is farther ventral to the anterior plate of the vomer than in *Moschorhinus;* (8) a wider posterior opening of the post-temporal fossa; (9) the greater development of intermediate and mastoid processes of the squamosal; the former covers the postero-dorsal process of the opisthotic in anterior view and the latter covers a large part of the mastoid process of the opisthotic in occipital view; (10) a greater participation of the supra-occipital in the margin of the foramen magnum. The dentary of *Promoschorhynchus* differs from that of *Moschorhinus* in the following characters: (1) the relatively slender bone is not markedly constricted behind the canine; (2) the part of the dentary participating in the formation of the symphysis is separated from the horizontal ramus by a much less pronounced mentum angulation, and the dentary is less thickened at this level; (3) the ascending ramus is relatively longer and the gonial angle is smaller. The dental formula of *Promoschorhynchus* is $\frac{5}{4}$ I, $\frac{1pC,\ 1C}{1C}$, $\frac{5-6}{6-?}$ PC; it differs from that of *Moschorhinus* in the slightly greater number of postcanines.

DESCRIPTION

The skull of *Promoschorhynchus platyrhinus* (R.C. No. 116) is of medium size with a strongly built snout which is relatively longer and less massive than that of *Moschorhinus*. The dorsal sur-

TABLE 1
The chief measurements (in mm) are:

	B.P.I. No. F.484/M.192	R.C. No. 116	G.S.P., K.C. No. R.85
1. Total length of the skull (reconstructed)	—	135 approx.	—
2. Maximum width (reconstructed)	—	100 approx.	—
3. Distance between the anterior border of the premaxilla and the anterior orbital border (reconstructed)	—	66 approx.	—
4. Breadth of the snout at the level of its maximal constriction (reconstructed)	40 approx.	39 approx.	31 approx.
5. Height of the snout at the same level (reconstructed)	30 approx.	—	25 approx.
6. Total length of the maxillary dentition	26 (right)	28 (right), 26 (left)	25 (right) approx.
7. Total length of the postcanine tooth-row	16 (right)	15,5 (right), 13,5 (left)	16 (right) approx.
8. Length of the anterior part of the palate, on the middle-line, between the anterior edge of the first incisor alveolar border and the posterior edge of the medial part of the transverse processes	—	76	—
9. Length between this point of the transverse processes and the posterior limit of the tubercula spheno-occipitalia	—	36	—
10. Length, on the middle-line, of the palatal plate of the premaxilla	14	—	—
11. Length of the anterior plate of the vomers, from the premaxillo-vomerine suture to its narrowest part (near the posterior end of the choanal opening) in the middle-line	25	25	—
12. Breadth of the vomer at the premaxillo-vomerine suture	13,5	13,5	—
13. Total length of the dentary, from dorsal point of the symphysis anterior to the incisors to the posterior angle of the coronoid process	—	107	—
14. Length of the horizontal ramus of the dentary from the base of the symphysis to the goniac angle	—	55	—
15. Length of the ascending ramus from the goniac angle to the posterior angle of the coronoid process	—	41	—

face of the skull is weathered; however the dorsal surface of the snout of the type specimen (B.P.I. No. F.484/M.192) is well preserved. The type specimen is used also for the description of the anterior part of the palate because this area in R.C. No. 116 is obscured by the presence of the lower jaw.

Note on Figures: The skull of R.C. No. 116 being little distorted, the drawings correspond to reconstructions, allowing for the asymmetry and the slight crushing of the posterior part of the skull. The palate of the type (B.P.I. No. F.484/M.192) has been represented in an earlier article (Mendrez, 1973, Fig. 7). The dorsal surface of the snout of R.C. No. 116 is reconstructed after the type.

I. SKULL

A. Dermal Bones

1. *Dorsal surface* (Fig. 1 and Pl. I. A)

In the type specimen (B.P.I. No. F.484/M.192) premaxillae, septomaxillae, maxillae, nasals and a small part of the prefrontal and frontal are preserved.

The premaxillae (*Pmx*), of which the nasal processes are missing, are little exposed in anterior and lateral view. They are covered by the septomaxilla (*Smx*) and the maxilla (*Mx*). The latter extends anteriorly to the level of the fourth incisor.

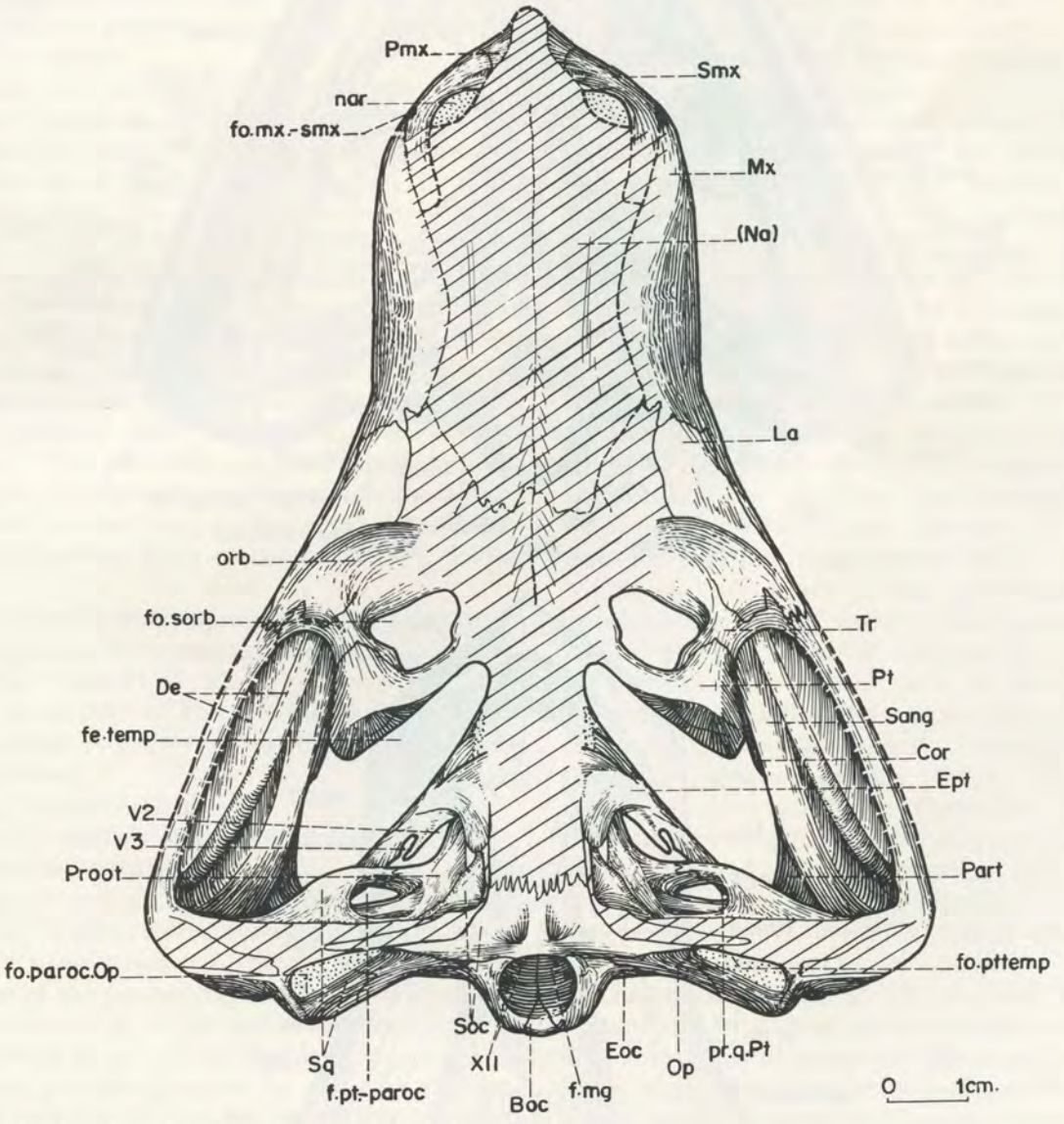

Fig. 1 *Promoschorhynchus platyrhinus*. RC. No. 116; dorsal view (x 1).
Boc, basioccipital; *Cor*, coronoid; *De*, dentary; *Eoc*, exoccipital; *Ept*, epipterygoid; *f.mg*, foramen magnum; *f.pt.-paroc*, pterygo-paroccipital foramen; *fe. temp*, fenestra temporalis; *fo.mx.-smx*, maxillo-septomaxillary fossa; *fo. paroc. Op*, paroccipital fossa of the opisthotic; *fo.pttemp*, posttemporal fossa; *fo,sorb*, suborbital fossa (or suborbital vacuity); La, lachrymal; *Mx*, maxilla; *(Na)*, impression of the nasal; *nar*, nare; *Op*, opisthotic; *orb*, orbit; *Part*, prearticular; *Pmx*, premaxilla; *pr.q.Pt*, quadrate process of the pterygoid; *Proot*, prootic; *Pt*, pterygoid; *Sang*, surangular; *Smx*, septomaxilla; *Soc*, supraoccipital; *Sq*, squamosal; *Tr*, transversum; *V2*, notch for the maxillary branch of the trigeminal nerve; *V3*, notch for the mandibular branch of the trigeminal nerve; *XII*, internal foramen for the hypoglossal nerve.

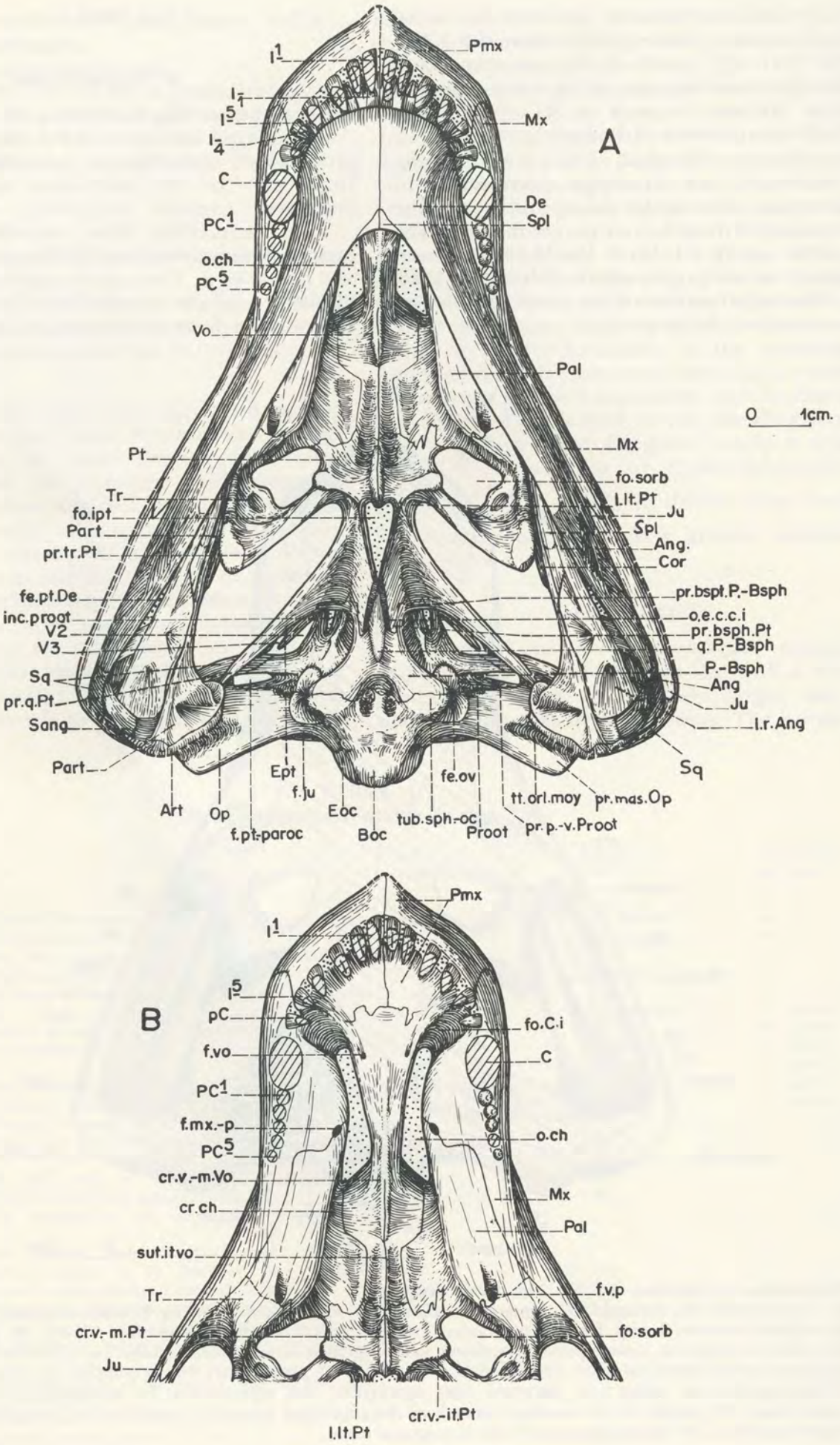
A
Pmx
I1
I1
I5
I4
C
PC1
o.ch
PC5
Vo
Mx
De
Spl
Pal
0 1cm.
Pt
Tr
fo.ipt
Part
pr.tr.Pt
fe.pt.De
inc.proot
V2
V3
Sq
pr.q.Pt
Sang
Part
Art
Op
Ept
f.ju
f.pt-paroc
Eoc
Boc
fe.ov
tub.sph-oc
Proot
tt.orl.moy
pr.p.-v.Proot
pr.mas.Op
Sq
fo.sorb
l.lt.Pt
Ju
Spl
Ang.
Cor
pr.bspt.P.-Bsph
o.e.c.c.i
pr.bsph.Pt
q.P.-Bsph
P.-Bsph
Ang
Ju
l.r.Ang
B
Pmx
I1
I5
pC
f.vo
PC1
f.mx.-p
PC5
cr.v.-m.Vo
cr.ch
sut.itvo
Tr
cr.v.-m.Pt
Ju
l.lt.Pt
fo.C.i
C
o.ch
Mx
Pal
f.v.p
fo.sorb
cr.v.-it.Pt

Fig. 2.

Fig. 2 *Promoschorhynchus platyrhinus*. RC. No. 116; *A:* complete ventral view with lower jaw *in situ* (x 1); *B:* palate, with lower jaw supposed to have been removed (x 1).
Ang, angular; *Art,* articular; *Boc,* basioccipital; *C,* canine; *Cor,* coronoid; *De,* dentary; *cr. ch, crista choanalis; cr.v.-it.Pt,* ventro-intermediate crest of the pterygoid; *cr.v.-m.Pt,* ventro-medial crest of the pterygoid; *cr.v.-m.Vo,* ventro-medial crest of the vomer; *Eoc,* exoccipital; *Ept,* epipterygoid; *f.ju,* jugular foramen; *f.mx.-p,* maxillo-palatine foramen; *f.pt.-paroc,* pterygo-paroccipital foramen; *f.v.p.,* foramen for the *vena palatina major; f.vo,* vomerine foramen; *fe.ov, fenestra ovalis; fe.pt.-De,* post-dentary fenestra; *fo.C.i,* fossa for the lower canine; *fo.ipt,* interpterygoid fossa; *fo.sorb,* suborbital fossa (or suborbital vacuity); I^1, first upper incisor; I_1, first lower incisor; I_4, fourth lower incisor; I^5, fifth upper incisor; *inc. proot, incisura prootica; Ju,* jugal; *l.lt.Pt,* lateral lamina of the pterygoid; *l.r.Ang,* reflected lamina of the angular; *Mx,* maxilla; *o.ch,* internal choanal opening; *o.e.c.c.i,* external opening of the canal of the internal carotid; *Op,* opisthotic; *P.-Bsph,* para-basisphenoid complex; *Pal,* palatine; *Part,* prearticular; PC^1, first upper postcanine; PC^5, fifth upper postcanine; *pC,* precanine; *Pmx,* premaxilla; *pr.bsph.Pt,* basisphenoid process of the pterygoid; *pr.bspt.P-Bsph,* basipterygoid process of the para-basisphenoid complex; *pr.mas.Op,* mastoid process of the opisthotic; *pr.q.Pt,* quadrate process of the pterygoid; *pr.tr.Pt,* transverse process of the pterygoid; *Proot,* prootic; *Pt,* pterygoid; *Sang,* surangular; *Spl,* splenial; *Sq,* squamosal; *sut.itvo,* intervomerine suture; *Tr,* transversum; *tt.orl.moy,* roof of the middle ear; *tub.sph.-oc, tuberculum spheno-occipitale; Vo,* vomer; *V2,* notch for the maxillary branch of the trigeminal nerve; V^3, notch for the mandibular branch of the trigeminal nerve.

The septomaxilla (*Smx*) is well developed and has a broad posterior process extending between the maxilla and the nasal.

The maxilla (*Mx*) is highest at a point opposite to the middle of the nasals. From this point the maxilla regularly slopes both forward and backward. Therefore, the nasals appear constricted in the middle. In *Moschorhinus* the maxilla reaches its maximum height at the level of the posterior end of the septomaxilla and this height remains constant to the level of the prefrontal, so that the nasals do not appear constricted. The snout of *Promoschorhynchus* is slightly constricted behind the canine; this is more noticeable in the upper part of the maxilla. This character has not been observed in *Moschorhinus*. The maxilla of *Promoschorhynchus* participates in the formatiom of the suborbital bar nearly as much as the jugal and extended probably as far as the posterior limit of the orbit (Fig. 3 and Pl. II. B).

In both genera, a mid-sagittal ridge is present in the posterior part of the nasal and the frontal.

2. *Occiput* (Fig. 4 and Pl. II. C).

Only the basal part of the occiput, belonging to the endocranium, is preserved in R.C. No. 116 and is described below.

3. *Cheek* (Fig. 3 and Pl. II. A—B)

The relatively narrow jugal (*Ju*) is represented by its anterior and suborbital portions.

Only a small part of the posterior area of the squamosal (*Sq*) is observable. Posteriorly (Fig. 3 and Pl. II. C) the squamosal contributes greatly to the lower margin of the post-temporal fossa. Within the temporal fenestra (Fig. 5) the antero-ventral process of the squamosal (*pr.a.-v.Sq*) is divided into two, the robust prootic process (*pr.proot.Sq*) and the slender epipterygoid process (*pr. ept.Sq*). A similar subdivision of the antero-ventral process has also been observed in *Moschorhinus* and in the Whaitsiidae.

The upper part of the quadratojugal (*Qj,* Fig. 2 and Pl. II. A—C) is well preserved and is broad. It is separated from the quadrate (*Q*) by the quadrate-quadratojugal foramen (*f.q.-qj*). The ventral part of the quadratojugal is weathered.

4. *Palate* (Fig. 2 A,B and Pl. I. B,C)

The palate of *Promoschorhynchus* is less specialized than that of *Moschorhinus,* but shows a sharper *crista choanalis* (*cr.ch*).

The relative length of the snout is reflected on the palate. In *Promoschorhynchus* the distance between the posterior edge of the medial part of the transverse processes of the pterygoid and the posterior limit of the *tubercula spheno-occipitalia* (Tab. 1, No. 9) equals only 47% of the length of the anterior part of the palate in the mid-line, between the anterior edge of the first incisor alveolar border and the posterior edge of the medial part of the transverse processes (Tab. 1, No. 8). This ratio is greater in *Moschorhinus* in which it varies from 61% to 68%. In *Moschorhinus,* the measurements have been taken on the four specimens in which the whole palate is available. The size of the specimen does not seem to influence this ratio.

The palatal plate of the premaxilla (*Pmx*) has approximately the same antero-posterior length both medially and laterally, whereas in *Moschorhinus* the lateral part of the plate is considerably longer than the medial part. Together with the maxilla, each premaxilla forms the roof of the fossa for the lower canine (*fo.C.i*). This fossa is not otherwise distinguishable from the long reniform choanal opening (*o.ch*). The sharp *crista choanalis* extends forward on the maxilla and reaches the anterior edge of the choanal opening. In *Moschorhinus* this crest is blunt and tapers to terminate at the level of the canine.

The vomers (*Vo.* Fig. 2B) are still well separated posteriorly by a clear intervomerine suture (*sut.itvo*). The anterior and posterior plates are situated at the same level dorsal to the *crista choanalis*. The anterior plate broadens anteriorly but to a lesser extent than in *Moscorhinus* and is oar-shaped rather than fan-shaped. The ventro-median crest (*cr.v.-m.Vo*) is very high and sharp. Two vomerine foramina (*f.vo*) are visible anteriorly.

The pterygoids (*Pt,* Fig. 2A) extend anteriorly to the level of the anterior border of the suborbital fossa (*fo.sorb*). They are remarkable because of the

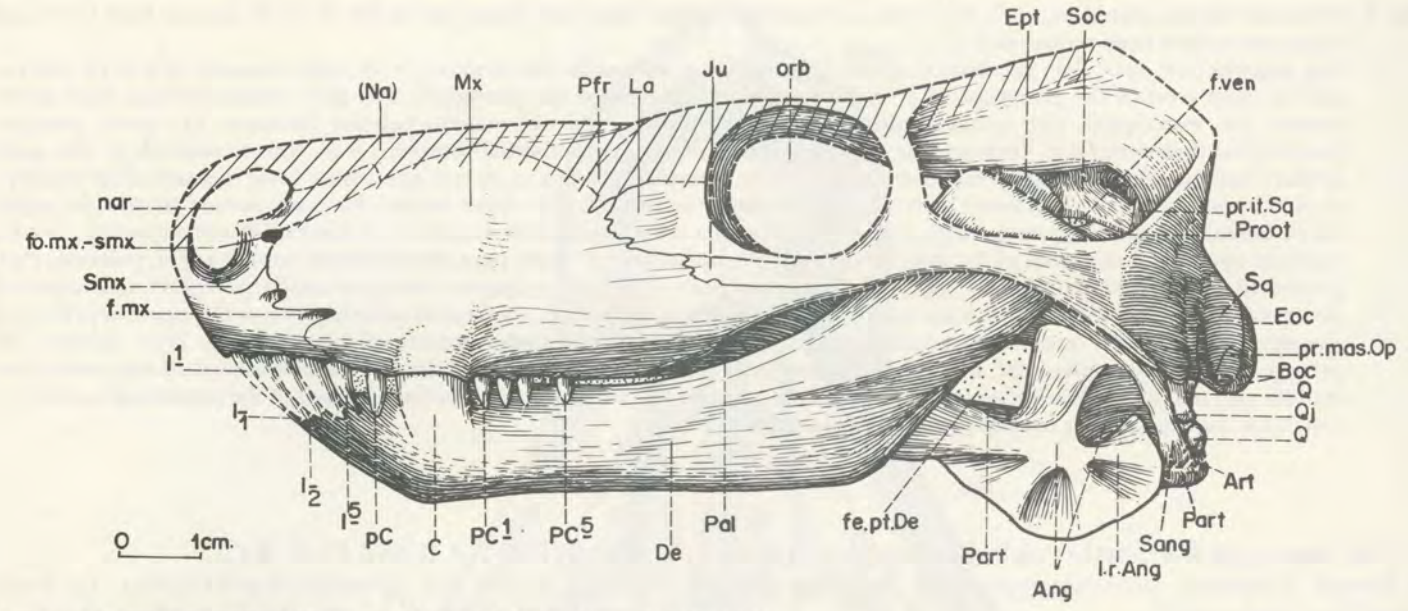

Fig. 3 *Promoschorhynchus platyrhinus.* RC. No. 116; left lateral view (x 1).
Ang, angular; *Art,* articular; *Boc,* basioccipital; *C,* canine; *De,* dentary; *Eoc,* exoccipital; *Ept,* epipterygoid; *f.mx,* maxillary foramen; *f.ven,* venous foramen; *fe.pt.-De,* post-dentary fenestra; *fo.mx.-smx,* maxillo-septomaxillary fossa; I^1, first upper incisor; I_1, first lower incisor, I_2, second lower incisor; I^5, fifth upper incisor; *Ju,* jugal; *l.r.Ang,* reflected lamina of the angular; *La,* lachrymal; *Mx,* maxilla; *(Na),* impression of the nasal; *nar,* nare; *orb,* orbit; *Pal,* palatine; *Part,* prearticular; *Pfr,* prefrontal; *pr.it.Sp,* intermediate process of the squamosal; *pr.mas.Op,* mastoid process of the opisthotic; PC^1, first upper postcanine; PC^5, fifth upper postcanine; *pC,* precanine; *Proot,* prootic; *Q,* quadrate; *Qj,* quadratojugal; *Sang,* surangular; *Smx,* septomaxilla; *Soc,* supraoccipital; *Sq,* squamosal.

prominence of the tuberosity at the posterior end of the ventro-intermediate crest of the pterygoid (*cr.v.-it.Pt*), and the very acute angle formed between the transverse (*pr.tr.Pt*) and the quadrate processes (*pr.-q.Pt*). The lateral lamina of the pterygoid (*l.lt.Pt*) is very small. The posterior edge of the transverse process seems to be in continuity with the edge of the quadrate process, while the edge of the tuberosity of the ventro-intermediate crest is continuous with the edge of the interpterygoid fossa (*fo.ipt*) (or "medial pterygoid crest" according to Barghusen's nomenclature (1968, pp. 6 and 41)). The lateral end of the concave transverse process is strongly swollen. The pterygoids of either side are closely approximated in front of the para-basisphenoid keel (*q.P.-Bsph*). The basisphenoid process (*pr.bsph.Pt*) extends anteriorly a little farther than the external opening of the internal carotid canal (*o.e.c.c.i.*). The lamina between the quadrate process and the basisphenoid process is strongly concave, bordered by the strong crest of the quadrate process.

The maxilla (*Mx.* Fig. 2B) is swollen medially to the canine (*C*) and is broadly extended medially to the postcanines (*PC*). In *Moschorhinus,* the contribution of the palatine (*Pal*) is much greater at the level of the postcanines. On the type of *Promoschorhynchus* (B.P.I. No. F. 484/M.192), this part of the maxilla is marked by shallow parallel grooves which correspond to the impressions of the lower postcanines ((*PCi*) in Mendrez, 1973, Fig. 7). In R.C. No. 116 there are six lower postcanines. In *Promoschorhynchus* the maxillo-palatine foramen (*f.mx.-p*) is situated more posteriorly than in *Moschorhinus.* Relative to the position of the anterior plate of the vomer, the *crista choanalis* is situated more ventrally than in *Moschorhinus.*

The maxilla carries one precanine, one canine and five postcanines.

The anterior and posterior parts of the palatine (*Pal*) are relatively narrow and the latter does not extend farther than the anterior border of the suborbital fossa.

The transversum (*Tr,* Fig. 2A,B) extends anteriorly a little farther than the anterior border of the suborbital fossa (*fo. sorb*). The crest of the transversum is separated from the suborbital vacuity by a short narrow and flat flange. The broader posterior area is marked by a strong dimple. Posteriorly the transversum does not extend far and its limit remains dorsal to the ventro-lateral swelling of the transverse process. In *Moschorhinus* the posterior limit of the transversum reaches the anterior limit of the swelling.

B. Endocranium

The morphology of the para-basisphenoid complex (*P.-Bsph,* Fig. 2) is typical of therocephalians. The basipterygoid process (*pr. bspt. P.-Bsph*) is incompletely covered by the pterygoid. The keel (*q.P.-Bsph*), partly broken, does not seem to have extended far ventrally. The tubercula spheno-occipitalia (*tub.sph.-oc*) are strong. The para-basisphenoid complex, together with the basioccipital (*Boc,* Fig. 7),

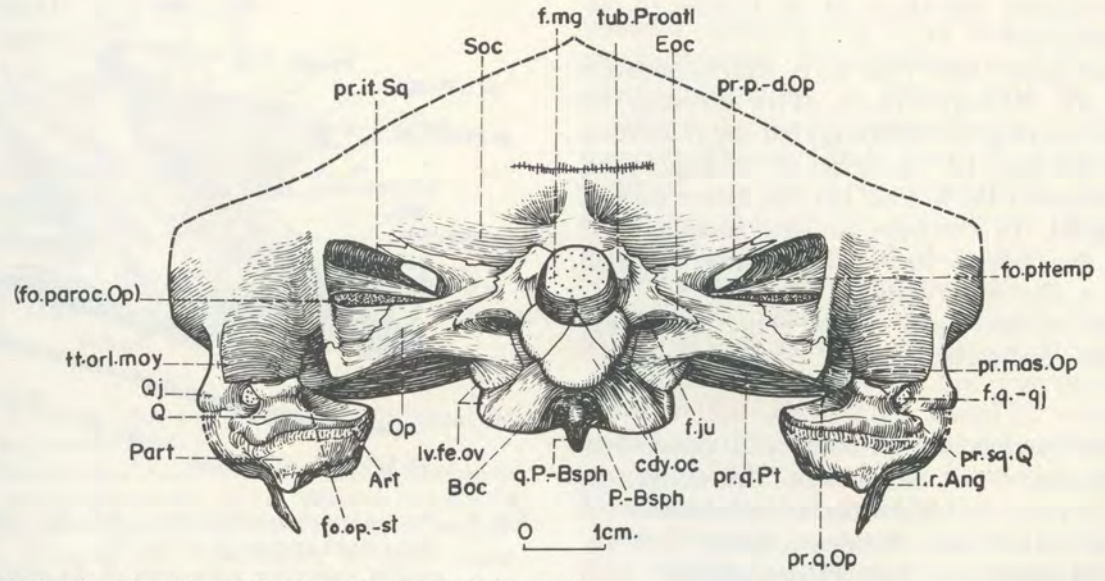

Fig. 4 *Promoschorhynchus platyrhinus.* RC. No. 116; occipital view (x 1).
Ang, angular; *Art,* articular; *Boc,* basioccipital; *cdy.oc,* occipital condyle; *Eoc,* exoccipital; *f.ju,* jugular foramen; *f.mg,* foramen; *(fo.paroc.Op),* paroccipital fossa of the opisthotic; *fo.pttemp,* posttemporal fossa; *lv.fe.ov,* 'lip' of the fenestra ovalis; *Op,* opisthotic; *Part,* prearticulr; *P.-Bsph,* para-basisphenoid complex; *pr.it.Sq,* intermediate process of the squamosal; *pr.mas.Op,* mastoid process of the opisthotic; *pr.p.-Op,* postero-dorsal process of the opisthotic; *pr.q.Op,* quadrate process of the opisthotic; *pr.q.Pt,* quadrate process of the pterygoid; *Q,* quadrate; *q.P.-Bsph,* keel of the para-basisphenoid complex; *Qj,* quadratojugal; *Soc,* supraoccipital; *tt.orl.moy,* roof of the middle ear; *tub.Proatl,* tuberosity for the articulation with the proatlas.

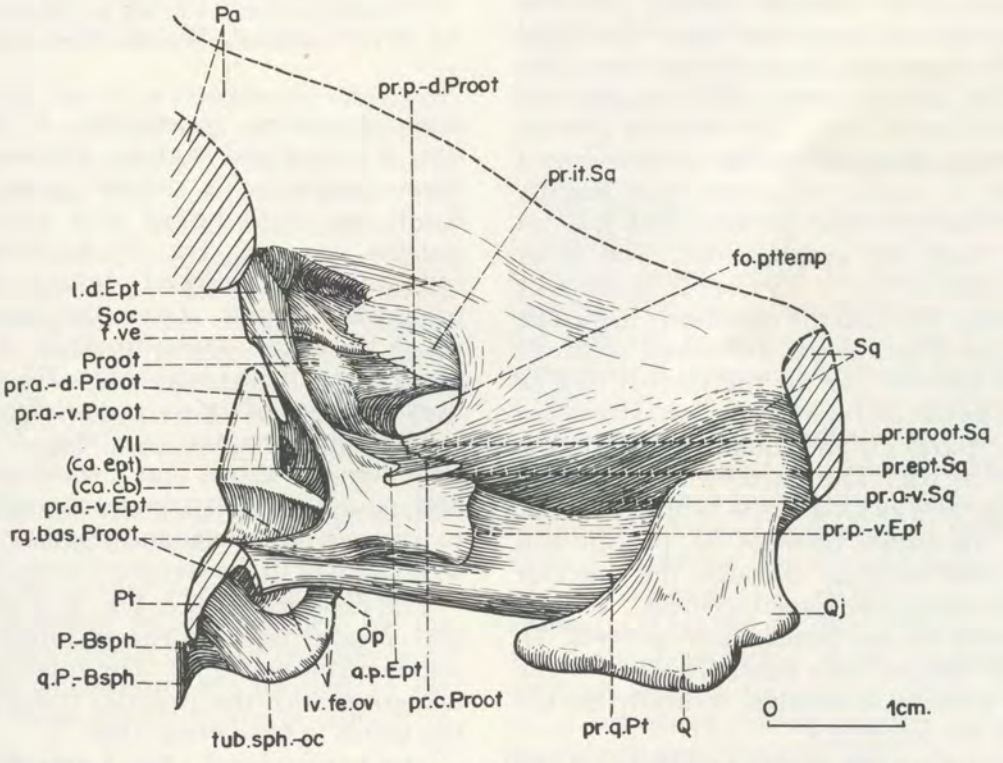

Fig. 5 *Promoschrohynchus platyrhinus.* RC. No. 116; Anterior view of the posterior wall of the left temporal fossa (x 5/3).
a.p.Ept, posterior apophysis of the epipterygoid; *(ca.cb),* brain cavity; *(ca.ept), cavum epiptericum; f.ven,* venous foramen; *fo.pttemp,* post-temporal fossa; *l.d.Ept,* dorsal lamina of the epipterygoid; *lv.fe.ov,* 'lip' of the *fenestra ovalis; Op,* opisthotic; *P.Nsph,* para-basisphenoid complex; *Pa,* parietal; *pr.a.-d.Proot,* antero-dorsal process of the prootic; *pr.a.-v.Ept,* antero-ventral process of the epipterygoid; *pr.a.-v.Proot,* antero-ventral process of the prootic; *pr.a.-v.Sq,* antero-ventral process of the squamosal; *pr.c.Proot,* central process of the prootic; *pr.ept.Sq,* epipterygoid process of the squamosal; *pr.it.Sq,* intermediate process of the squamosal; *pr.p.-d.Proot,* postero-dorsal process of the prootic; *pr.p.-v.Ept,* postero-ventral process of the epipterygoid; *pr.proot.Sq,* prootic process of the squamosal; *pr.q.Pt,* quadrate process of the pterygoid; *Proot,* prootic; *Pt,* pterygoid; *Q,* quadrate; *q.P.-Bsph,* keel of the para-basisphenoid complex; *Qj,* quadratojugal; *rg.bas.Proot,* basal area of the prootic; *Soc,* supraoccipital; *Sq,* squamosal; *tub.sph.-oc, tuberculum spheno, occipitale; VII,* foramen for the facial nerve.

form approximately one third of the border of the fenestra ovalis (*fe.ov*).

The epipterygoid (*Ept,* Fig. 6) is much broader than that of *Moschorhinus*. The posterior apophysis, separating the openings for the maxillary (*V2*) and mandibular (*V3*) branches of the trigeminal nerve, is positioned fairly low, on the lower half of the epipterygoid. In contrast, in *Moschorhinus* it is situated on the upper half. The postero-ventral process (*pr.p.-v.Ept*) is very high.

The cavum epiptericum (*ca.ept,* Fig. 5) is very broad in *Promoschorhynchus*.

The otic bones

In *Promoschorhynchus* the prootic and opisthotic are distinguishable from each other. This condition has been observed by Mendrez in a number of therocephalian families: Ictidosuchidae (1972a, p. 201), Whaitsiidae, Pristerognathidae and Moschorhinidae (1974). It is probably a general feature of the Therocephalians.

The prootic (*Proot,* Fig. 7) is fairly well preserved. It shows the general therocephalian morphological pattern (*Ptomalestes* excluded, which has an additional process) as far as this is known. The basal area of the prootic (*rg.bas*) is in contact with the para-basisphenoid complex (*P.-Bsph*) and forms a third of the border of the fenestra ovalis (*fe.ov*). The antero-ventral process (*pr.a.-v*) is strong with ventral and lateral faces separated by a sharp crest. The foramen for the facial nerve (*VII*) is situated posteriorly to the lateral face. The incisura prootic (*inc.proot*) is narrow posteriorly. The antero-dorsal process (*pr.a.-d*) is positioned above and slightly lateral to the antero-ventral process and has no sutural contact with the epipterygoid. The short postero-dorsal process (*pr.p.-d.Proot*) is in contact with the squamosal (*Sq*) and the opisthotic (*Op*). The long central process (*pr.c.Proot*), bordered ventrally and dorsally by grooves, forms the medial half of the bar anterior to the pterygo-paroccipital foramen (*f.pt.-paroc,* Figs. 1 and 2). The squamosal forms the lateral half of this bar. The latero-ventral process (*pr.p.-v.Proot,* Fig. 2) is as long as the central process. In dorsal view, the suture between the prootic and the opisthotic runs laterally through the anterior half of the post-temporal fossa (*fo.pttemp*). It then emerges anteriorly to the paroccipital process. In ventral view, the suture runs medially towards the fenestra ovalis where it continues ventrally on the dorsal border of the fenestra.

The opisthotic (*Op*) also forms one-third of the margin of the fenestra ovalis. Its dorsal process (*pr.p.-d.Op,* Fig. 4) is thin and elongated; it is completely covered anteriorly by the intermediate process of the squamosal (*pr.it.Sq,* Fig. 5) in contrast to the situation observed in *Moschorhinus* S.A.M. No. K. 118 (Mendrez, 1974, Figs. 6—7). The paroccipital process is very strong and is marked ventrally by a very deep and narrow groove (*tt.orl.may*) separating the quadrate process (*pr.q.Op*) from the

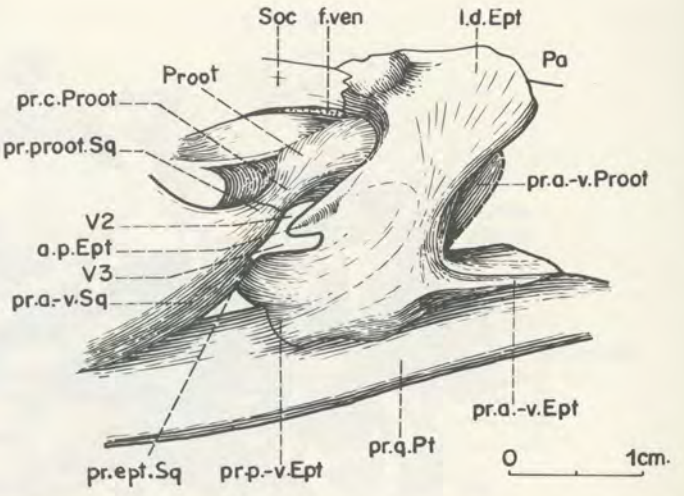

Fig. 6 *Promoschrohynchus platyrhinus.* RC. No. 116; lateral view of the right epipterygoid (x 1/3).
a.p.Ept, posterior apophysis of the epipterygoid; *f.ven,* venous foramen; *l.d.Ept,* dorsal lamina of the epipterygoid; *Pa,* parietal; *pr.a.-v.Ept,* antero-ventral process of the epipterygoid; *pr.a.-v.Proot,* antero-ventral process of the prootic; *pr.a.-v.Sq,* antero-ventral process of the squamosal; *pr.c.Proot,* central process of the prootic; *pr.ept.Sq,* epipterygoid process of the squamosal; *pr.p.-v.Ept,* postero-ventral process of the epipterygoid; *pr.proot.Sq,* prootic process of the squamosal; *pr.q.Pt,* quadrate process of the pterygoid; *Proot,* prootic; *Soc,* supraoccipital, *V2,* notch for the maxillary branch of the trigeminal nerve; *V3*, notch for the mandibular branch of the trigeminal nerve.

mastoid process (*pr.mas.Op*). In *Moschorhinus* this area is broad and shallow. The mastoid process of *Promoschorhynchus* is slender, even taking into account the crushing of that area. The quadrate process (*pr.q.Op,* Fig. 4) is more massive. The opisthotic is marked ventro-anteriorly by a triangular groove above the fenestra ovalis into which the stapes probably fitted. A long and broad paroccipital fossa (*fo.paroc.Op,* Fig. 4) is found on the dorsal surface of the paroccipital process.

The supraoccipital (*Soc,* Fig. 4) is damaged but what remains shows that it was tripartite, fairly high and broad. It participates broadly in the upper margins of the foramen magnum (*f.mg*). It is also well exposed in the temporal fossa (Figs. 1, 3 and 5).

The exoccipital (*Eoc,* Fig. 4) is tripartite. Its long and slender lateral process forms the roof of the jugular foramen (*f.ju*). The tuberculum for the articulation with the proatlas (*tub.Proatl*) is damaged but seems to have been large.

The basioccipital (*Boc*) forms slightly more than one third of the occipital condyle. In dorsal view it is visible posteriorly, but more anteriorly, at the level of the foramen magnum (*m.mg*), it is covered by the united exoccipitals. Two internal foramina for the hypoglossal nerve (*XII,* Fig. 1) open through the exoccipitals on each side. Ventrally, the basioccipital participates in the formation of the strong tuberculum spheno-occipitale (*tub.sph.-oc,* Fig. 2) together with the para-basisphenoid complex. Of the four

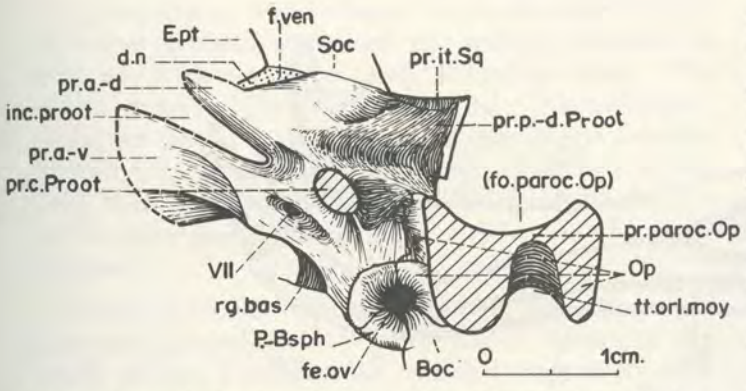

Fig. 7 *Promoschrohynchus platyrhinus.* RC. No. 116; lateral view of the left prootic (x 5/3).
Boc, basioccipital; *d.n.,* dorsal notch; *Ept,* epipterygoid; *f.ven,* venous foramen; *fe.ov, fenestra ovalis; (fo. paroc.Op),* paroccipital fossa of the opisthotic; *inc.proot, incisure prootica; Op,* opisthotic; *P.-Bsph,* parabasisphenoid complex; *pr.a.-d,* antero-dorsal process; *pr.a.-v,* antero-ventral process; *pr.c.Proot,* central process of the prootic; *pr.it.Sq,* intermediate process of the squamosal; *pr.p.-d.Proot,* postero-dorsal process of the prootic; *pr.paroc.Op,* paroccipital process of the opisthotic; *rg.bas,* basal area of the prootic; *Soc,* supraoccipital; *tt.orl.moy,* roof of the middle ear; *VII,* foramen for the facial nerve.

bones surrounding the fenestra ovalis, the basioccipital participates least in the formation of its margin.

The quadrate (Q, Fig. 4) is posteriorly damaged. It can be observed in occipital view and medial view. In addition, in dorsal view the left quadrate is visible because the squamosal has weathered away. The squamosal process (*pr.sq.Q*) has a short narrow and thick base which is visible in occipital view. More dorsally, it spreads laterally to form a flange which meets the quadratojugal. This flange is convex posteriorly. The opisthotic process appears fairly short, but the floor of the opisthotic-stapes fossa (*fo.op.-st*) is widely expanded medially. The quadrate-quadratojugal foramen (*f.q.-qj*) is broad.

C. Principal fossae and openings of the posterior part of the skull

The interpterygoid vacuity (*fo.ipt,* Fig. 2) is heart-shaped with its anterior margin divided by the bulging of the ventro-medial crest of the pterygoid (*cr.v.-m.Pt*). Its lateral margins are formed by the medial pterygoid crests which converge almost to meet posteriorly.

The fenestra ovalis (*fe.ov,* Fig. 7) is bordered by four bones (as said above): the prootic forms one third, the opisthotic forms one third and the parabasisphenoid complex, along with a minor contribution from the basioccipital, forms the remaining third of the border.

The posterior opening of the post-temporal fossa (*fo.pttemp,* Fig. 4) is broad and triangular-shaped; its border is formed by equal contributions from the squamosal and the opisthotic. The border of the anterior opening (Fig. 5) of this fossa is formed by the squamosal, the opisthotic and the prootic. The anterior opening is about half the size of the posterior one and is situated more medially, so that the two openings only partly face one another. In contrast, in the pristerognathid *Ptomalestes* the anterior opening is completely medial to the posterior opening and this latter is thus placed behind a sheet of the squamosal.

The paroccipital fossa (*fo.paroc.Op,* Fig. 4) is almost as long as the post-temporal fossa.

The anterior wall of the pterygo-paroccipital foramen (*f.pt.-paroc,* Figs. 1 and 2), which is formed by the central process of the prootic and the prootic process of the squamosal is narrow in its vertical dimension as in *Moschorhinus.*

The foramen magnum (Fig. 4) is bordered by the exoccipitals and the supraoccipital, which makes a greater contribution than in *Moschorhinus.*

The jugular foramen (Fig. 4) is bordered by two bones: the exoccipital and the opisthotic.

II. LOWER JAW (Figs. 3 and 8)

The lower jaw of *Promoschorhynchus* is characterized by a long dentary (*De*) of which the coronoid process extends above the level of the zygomatic arch. In addition, the postero-ventral corner of the coronoid process is separated by a short distance only from the squamosal.

A. Membrane bones

The dentary's horizontal ramus (Fig. 3) is relatively slender and does not show the dorso-ventral constriction which exists in *Moschorhinus* behind the canines. The coronoid process is thick. The part of the dentary participating in the formation of the symphysis is separated from the horizontal ramus by a very slight angulation. Posteriorly the horizontal ramus is separated from the ascending ramus by a wide goniac angle. The lateral surface of the coronoid process is marked by a slight groove anterior to the well-defined post-dentary fenestra (*fe.pt.-De*). Even if distortion is taken into account, the dentary of *Moschorhinus* differs from that of *Promoschorhynchus:* the "mentum" area of *Moschorhinus* is much more massively developed; on both sides a thickening of the dentary bulges in a manner comparable to that of the gorgonopsians—though not so pronounced and not median. The ascending ramus is relatively shorter in *Moschorhinus* and is separated from the horizontal ramus by a greater angle. The ratio between the length of the ascending ramus (Tab. 1, No. 14) and that of the horizontal ramus (Tab. 1, No. 15) is approximately 60% in *Moschorhinus* (B.P.I. No. F.2788/M.378) and approximately 82% in *Promoschorhynchus* (R.C. No. 116). These ratios are only given as an indication, as lack of specimens precludes the study of variation in either genus.

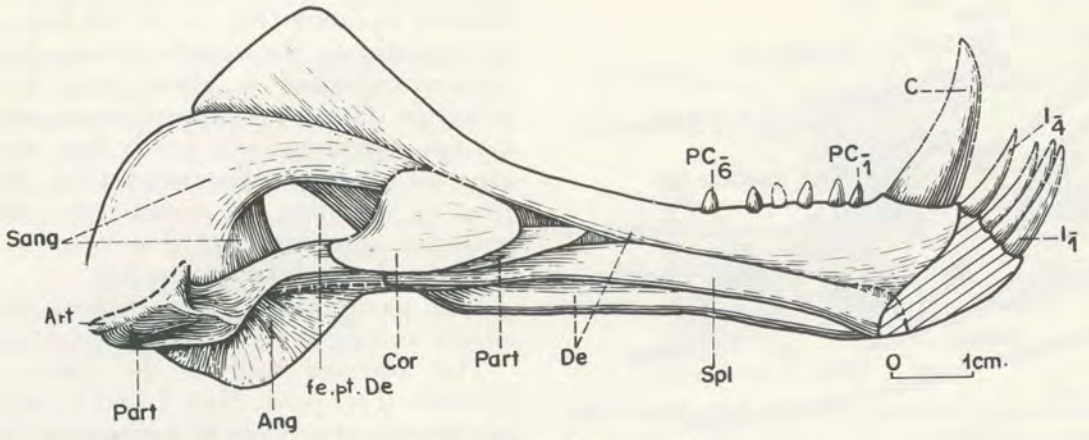

Fig. 8 *Promoschorhynchus platyrhinus*. RC. No. 116; medial view of the left mandible.
Ang, angular; *C*, canine; *Cor*, coronoid; *De*, dentary; *fe.pt.-De*, post-dentary fenestra; I_1, first lower incisor; I_4, fourth lower incisor; *Part*, prearticular; PC_1, first lower postcanine; PC_6, sixth lower postcanine; *Sang*, surangular, *Spl*, splenial.

The angular (*Ang*) and its reflected lamina have the typical therocephalian morphology with its pattern of bulges and grooves.

The splenial (*Spl*, Figs. 2A and 8) is an elongated bone participating in the formation of the lower part of the symphysis. Its posterior extent cannot be determined because it is broken slightly beyond the goniac angle.

The coronoid (*Cor*) is only partially visible in the specimen examined, but is elongated antero-posteriorly.

The surangular (*Sang*) is also only partly visible but its morphology appears to conform with the general therocephalian pattern.

The prearticular (*Part*) is characterized by the height and the sharpness of the buttress linking its vertical lamina to its ventral plate which covers the articular.

B. Cartilage bone

The area corresponding to the articular is too damaged to show any details.

III. DENTITION

The upper dental formula is identical in the type specimen (B.P.I. No. F.484/M.192) and the more complete specimen of the Rubidge collection (R.C. No. 116): 5I, 1pC, 1C, 5PC. These two specimens are almost identical in size. The specimen in the Keyser collection (G.S.P., K.C. No. R.85) which here is considered as a probable *Promoschorhynchus* has the following dental formula: 1pC, 1C, 6PC. This specimen is slightly smaller than the other two, so the number of postcanines may be reduced during growth, without affecting the length of the post-canine row (Tab. 1, No. 7).

The lower dental formula is 4I, 1C, 6PC. The greater number of postcanines in the lower jaw than in the maxilla is a very common feature amongst the therocephalians.

Very little can be said about the teeth because they are damaged. Both upper and lower incisors show labial facets extending half of their length from the tip. The fifth upper incisor is smaller than the others, but still larger than the precanine which in turn is bigger than the postcanines.

The postcanines seem to be simple cones. The single upper canines, as preserved, are large. The mesio-distal diameter of each canine is slightly larger than the labio-buccal diameter.

IV. DISCUSSION

Brink (1954, pp. 43—45, Fig. 2) when creating the genus *Promoschorhynchus* noted two points of resemblance with *Moschorhinus:* a mid-sagittal ridge on the nasal and frontal and the dimensions of the external nares. He noted one point of dissimilarity: the different proportions of the snout. He also considered that *Promoschorhynchus* agrees with *Moschorhynchus* in its general proportions and in the dimensions of the external nares. In addition, he concludes that *Promoschorhynchus* had no lower postcanine but possessed a palate "as far developed as in *Whaitsia*". He (p. 58) also concluded that *Promoschorhynchus* "evolved from *Moschorhinus*" and that "*Whaitsia* branched from *Promoschorhynchus* fairly early and *Moschorhynchus* much later". All the genera quoted above were included in the Whaitsiidae by Haughton and Brink (1954, pp. 147—151) and Watson and Romer (1956, p. 70).

In 1958 (p. 38—39), Brink divided the former family into Whaisiidae proper and Moschorhinidae. He then observed that "the aberrant *Whaitsia pricei*" may turn out to be a *Moschorhynchus* and this genus, with *Promoschorhynchus,* could then be included in the Moschorhinidae. He included *Notaelurops* in *Notosollasia,* doubting the existence of any difference between this latter and *Whaitsia.*

Concerning the South African Whaitsiids, Kitching (1972, thesis, p. 69) states that: "the marked similarity in the skull morphology, irrespective of minor individual variations, has led the author and others to conclude that the genera

Aneugomphius, Notosollasia and *Moschorhynchus* represent growth stages of the genus *Whaitsia,* as well as *Whaitsia pricei* and *Whaitsia major.* The other genera *Theriognathus* and *"Notaelurops"* based on single badly preserved specimens are also included in *Whaitsia.* It has been observed in the field that *"Notosollasia"* and *Whaitsia* normally occur in close association in the field or in the same horizon[11].

Mendrez (1973b, in press and 1974) recognizes only one valid genus for the Whaitsiidae of Tanzania and South Africa: *Theriognathus,* which has priority over *Whaitsia* and which, after further preparation, shows all the essential characteristics of *Whaitsia* for that part of the specimen which is preserved. *Theriognathus* is considered then as including *Hyenasuchus* as well as *Alopecopsis, Aneugomphius, Moschorhynchus, Notoaelurops, Notosollasia* and *Whaitsia* (including *W. pricei*). The differences between the Whaitsiidae and the Moschorhinidae have been emphasized.

In the Moschorhinidae, Kitching (1972, thesis, p. 70) does not accept the validity of the genus *"Promoschorhynchus platyrhinus,* based on a distorted snout . . . " and coming " . . . from the same horizon and exposure on the slopes of Compassberg that had previously yielded two specimens of the genus *Moschorhinus".* He concludes that "additional preparation to *Promoschorhynchus platyrhinus, Moschorhinus warreni* and *Cerdops burgheri* has revealed that these specimens are juvenile stages of *Moschorhinus kitchingi"* as well (possibly) as *Hewittia.*

It has been shown by Mendrez (1973, Fig. 7, in press) that the palate of the type specimen of *Promoschorhynchus* is very different from that described by Brink but is close to that of *Moschorhinus* though clearly distinguishable. The palate of the second specimen quoted by Mendrez (id, Fig. 8) agrees with that of the type. Further study of the latter specimen gives additional points of comparison between *Moschorhinus* and *Promoschorhynchus* and leads to the conclusion that they are different genera.

Mendrez (1974) has discussed also the composition of the South African Moschorhinidae, subfamily Moschorhininae which can be summarized as follows:

Moschorhinus is almost certainly synonymous with *Tigrisuchus. Tigrisuchus* is represented by the anterior half of the snout and shows a structure identical to that of *Moschorhinus;* however, the precanine formula is uncertain.

Cerdops is apparently very closely related to *Moschorhinus,* but is more lightly built if one compares specimens of the same size belonging to these two genera. The snout is much less massive and the suborbital bar and the postorbital and zygomatic arches are more slender. the precanine formula is shorter. What is available of the palate compares favourably with that of *Moschorhinus,* but the part of it anterior to the canines is obstructed by the lower jaw.

Hewittia has been compared to *Moschorhinus* on the bais of Brink's dentition (1958, pp. 37—38, Figs. 14—15) in Mendrez (1974) who concludes that it is better to leave it as a separate genus since the type specimen is now lost.

CONCLUSION

At present, the South African Moschorhinidae include five genera of which one is very doubtful: *Tigrisuchus* which is probably a synonym of *Moschorhinus;* if this can be proved *Tigrisuchus* has priority. Of the four other genera, *Promoschorhynchus* appears to be the most different from *Moschorhinus;* on the one hand, it has a relatively longer snout, a larger palatal plate of the premaxillae and a narrower anterior plate of the vomer, but, on the other hand, it is more advanced in having a broader epipterygoid and a sharper *crista choanalis.*

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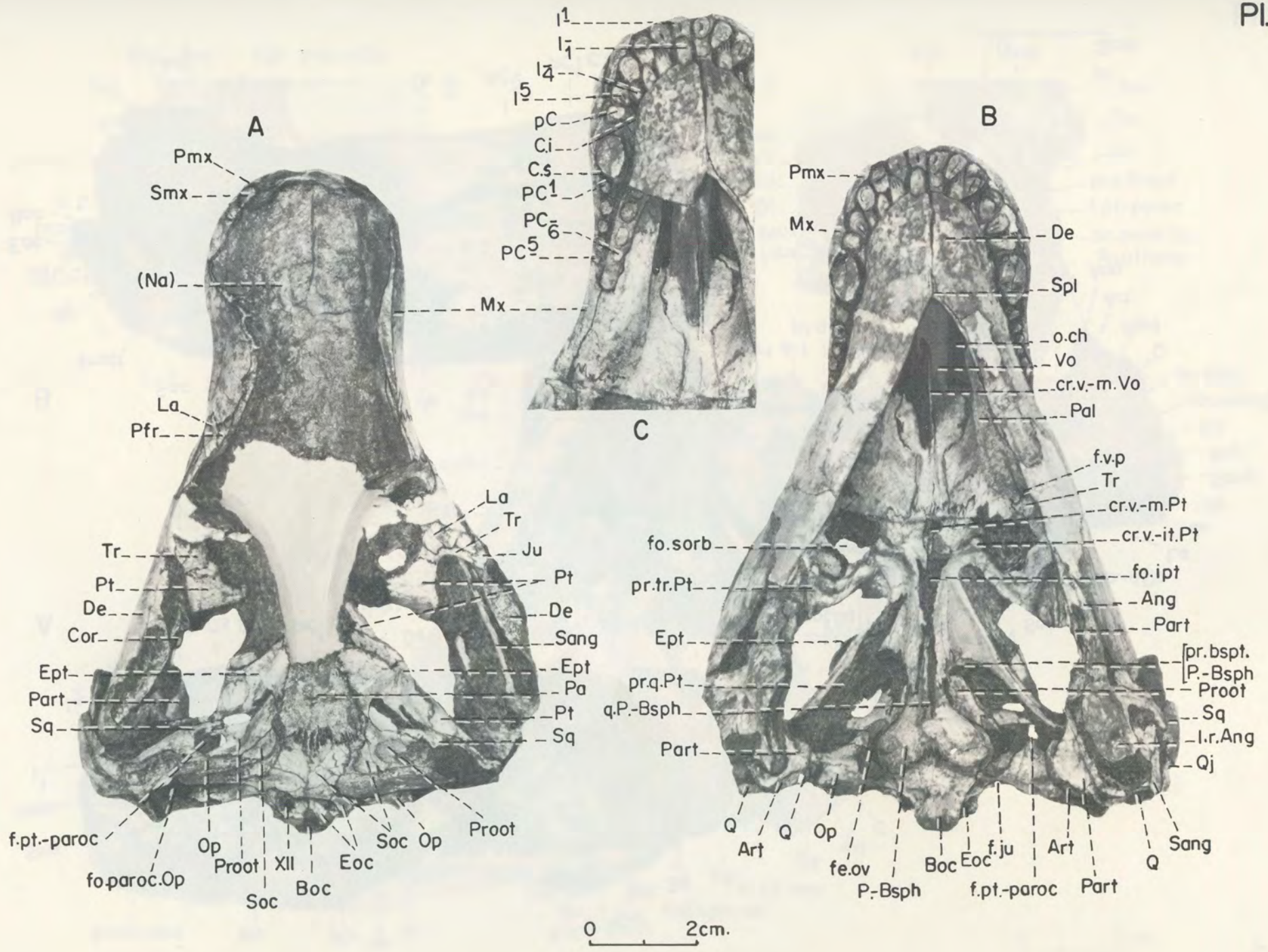
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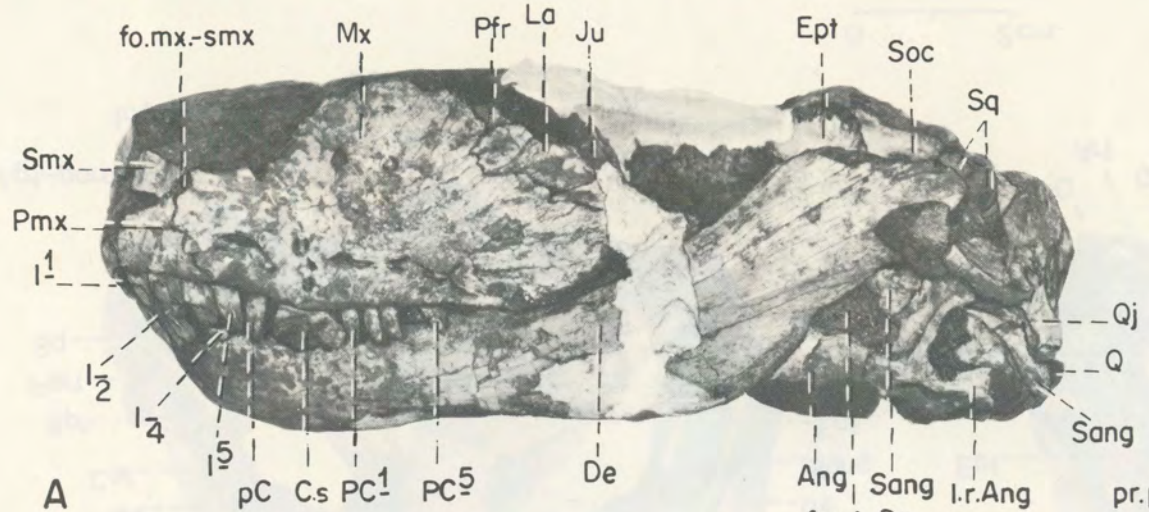
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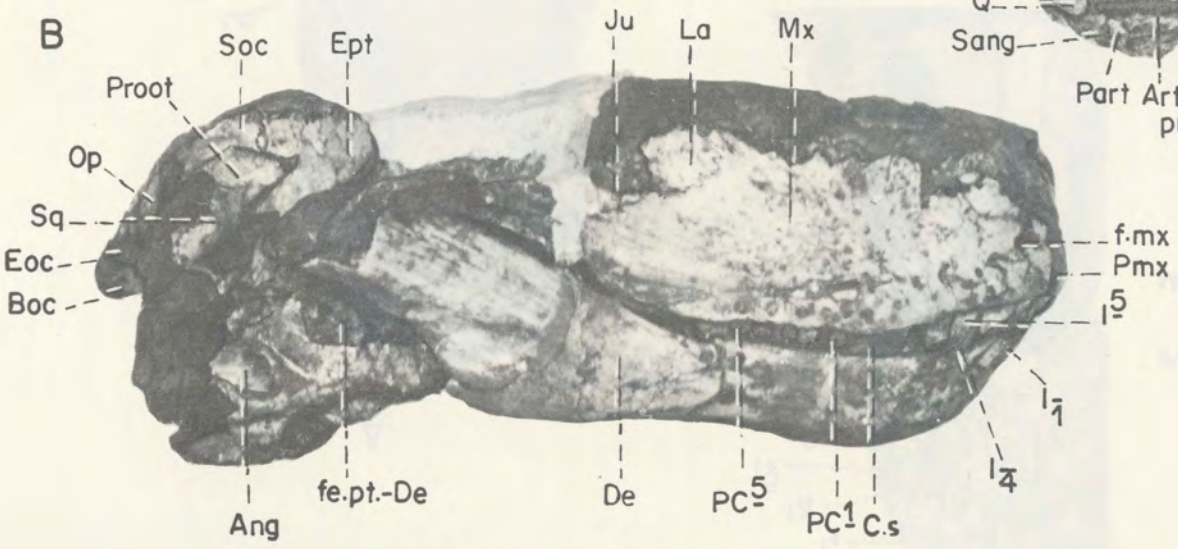
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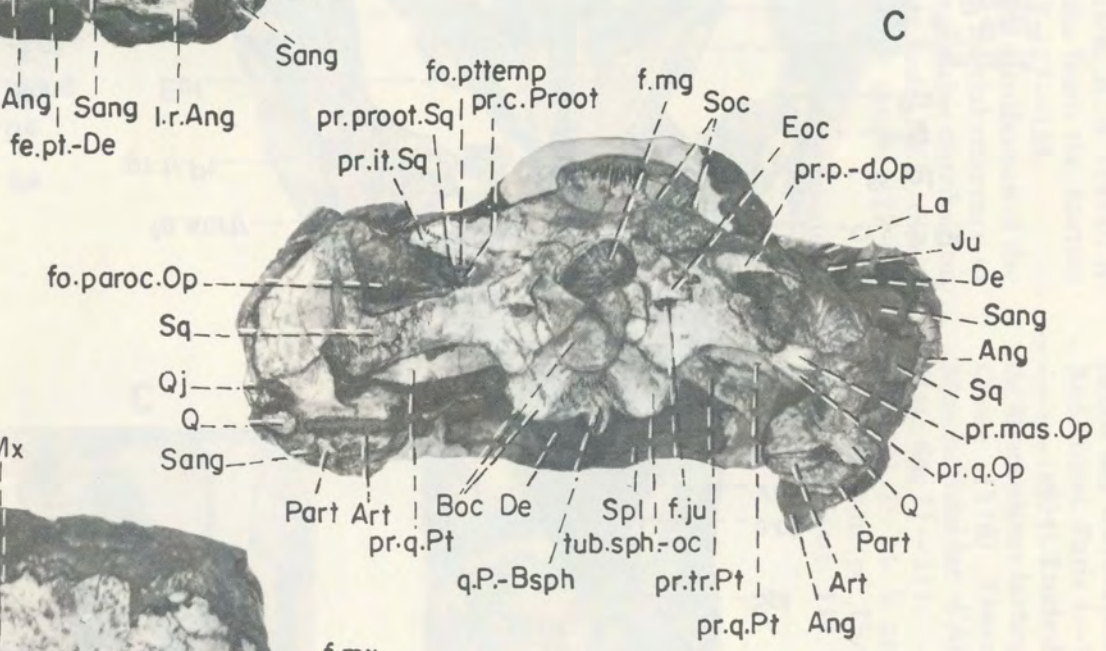
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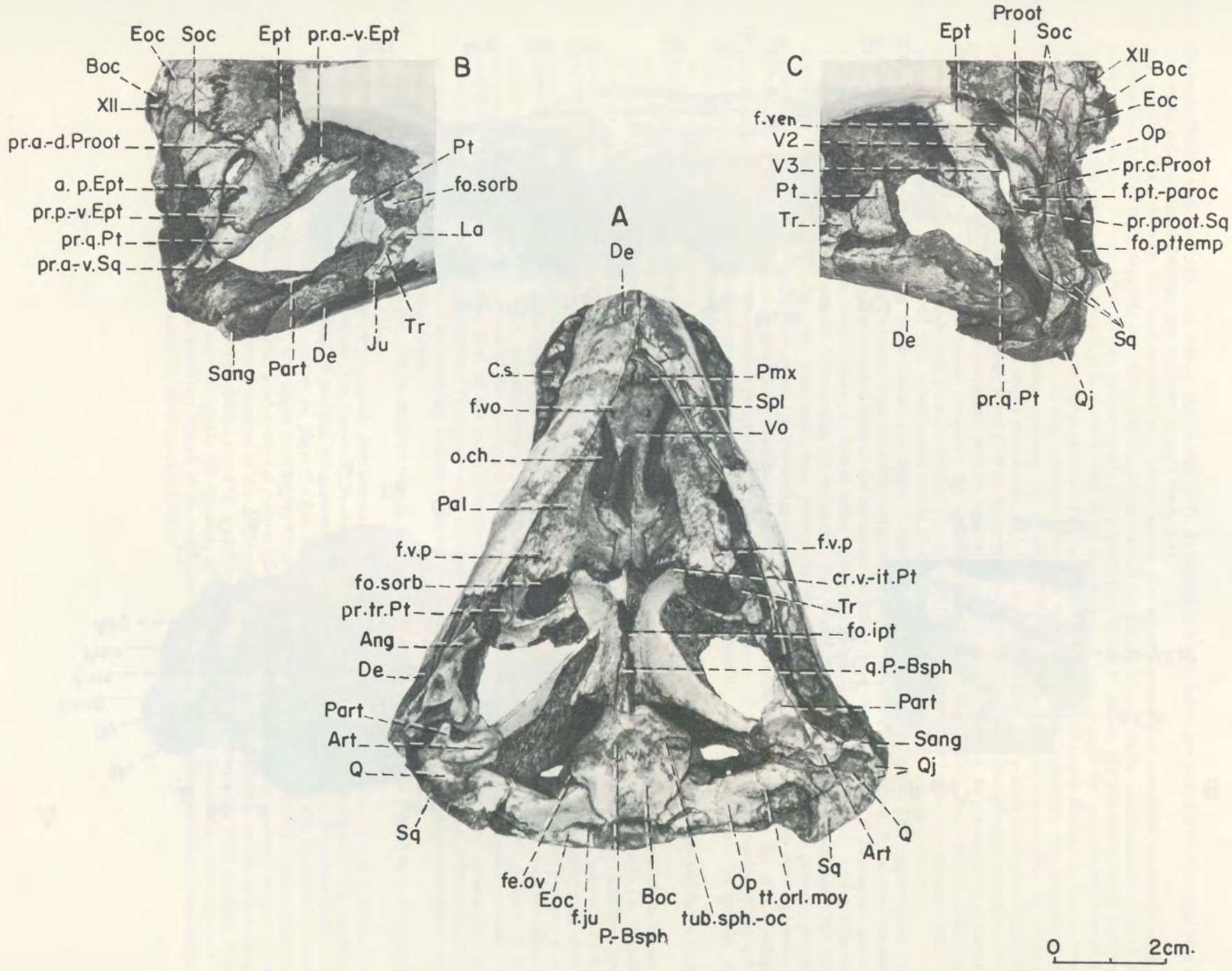
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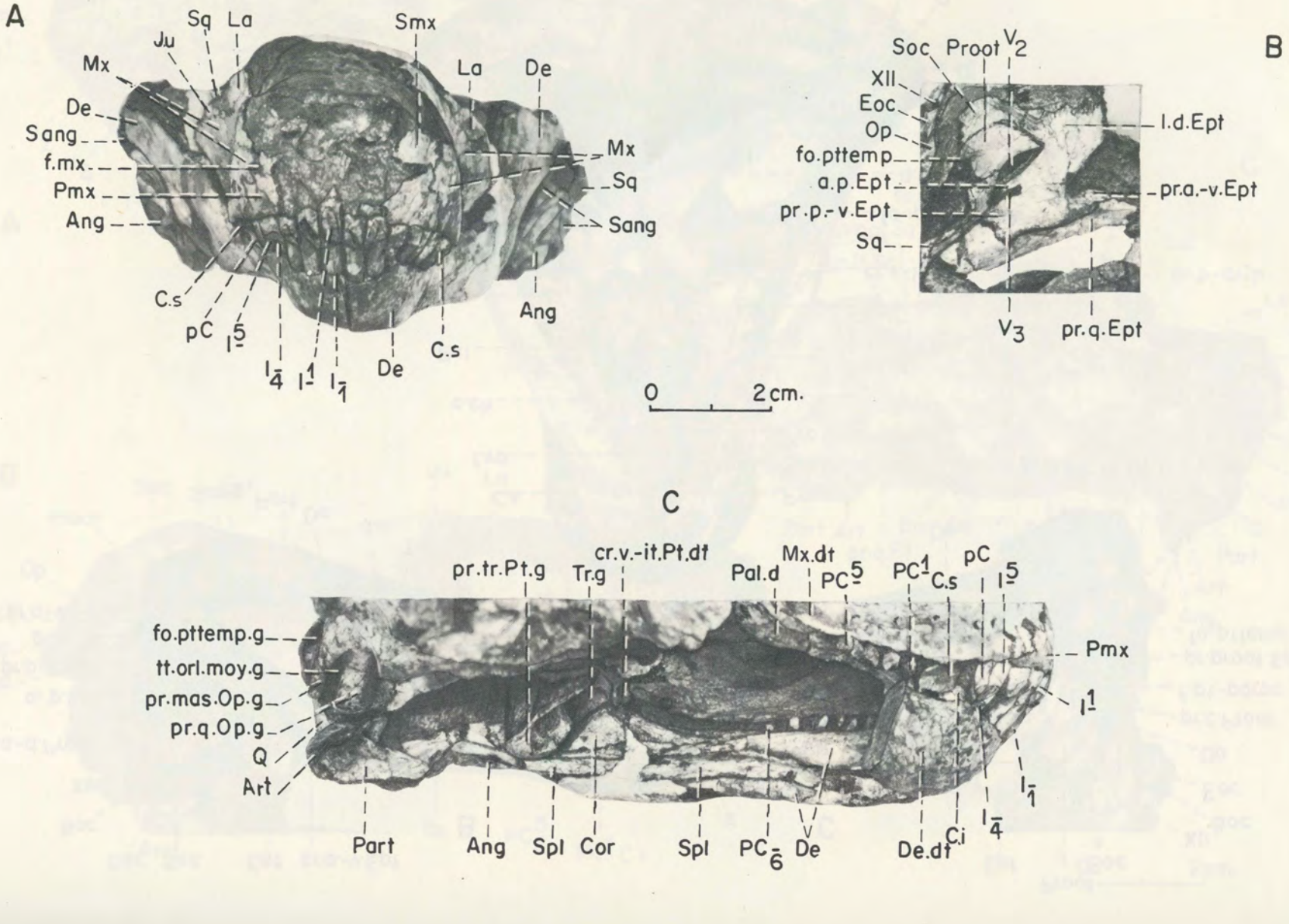
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Plate I *Promoschorhynchus platyrhinus*. RC. No. 116; *A*: dorsal view (x 1); *B:* ventral view with lower jaw in situ (x1); *C:* ventral view of part of the palate, part of the right jaw removed along a crack (x 1).
Ang, angular; *Art*, articular; *Boc*, basioccipital; *C.i.*, lower canine; *C.s*, upper canine; *Cor*, coronoid; *cr.v.-it.Pt*, ventro-intermediate crest of the pterygoid; *cr.v.-m.Pt*, ventro-median crest of the pterygoid; *cr.v.-m.Vo*, ventro-median crest of the vomer; *De*, dentary; *Eoc*, exoccipital; *Ept*, epipterygoid; *f.ju*, jugular foramen; *f.pt.-paraoc*, pterygo-paroccipital foramen; *f.v.p.*, foramen for the *vena platina major; fe.ov, fenestra ovalis; fo.ipt*, interpterygoid fossa; *fo.paroc.Op*, paroccipital fossa of the opisthotic; *fo.sorb*, suborbital fossa (or suborbital vacuity); I^1, first upper incisor; I_1, first lower incisor; I_4, fourth lower incisor; I^5, fifth upper incisor; *Ju*, jugal; *l.r.Ang*, reflected lamina of the angular; *La*, lachrymal; *Mx*, maxilla; *(Na)*, impression of the nasal; *o.ch*, internal choanae opening; *Op*, opisthotic; *P.-Bsph*, para-basisphenoid complex; *Pa*, parietal; *Pal*, palatein; *Part*, prearticular; PC^1, first upper postcanine; PC^5, fifth upper postcanine; PC_6, sixth lower postcanine; *pC*, precanine; *Pfr*, prefrontal; *Pmx*, premaxilla; *p.bspt.P.-Bsph*, basipterygoid process of the para-basisphenoid complex; *Proot*, prootic; *pr.q.Pt*, quadrate process of the pterygoid; *pr.tr.Pt*, transverse process of the pterygoid; *Pt*, pterygoid; *Q*, quadrate; *q.P.-Bsph*, keel of the para-basisphenoid complex; *Qj*, quadrato-jugal; *Sang*, surangular; *Smx*, septomaxilla; *Soc*, supraoccipital; *Spl*, splenial; *Sq*, squamosal; *Tr*, transversum; *Vo*, vomer; *XII*, internal foramen for the hypoglossal nerve.

Plate II *Promoschorhynchus platyrhinus*. RC. No. 116; *A;* left lateral view (x 1); *B:* right lateral view (x 1); *C:* occipital view (X 1).
Ang. angular; *Art*, articular; *Boc*, basioccipital; *C.s*, upper canine; *De*, dentary; *Eoc*, exoccipital; *Ept*, epipterygoid; *f.ju*, jugular foramen; *f.mg*, foramen magnum; *f.mx*, maxillary foramen; *fe.pt.-De*, post-dentary fenestra; *fo.mx.-smx*, maxillo-septomaxillary fossa; *fo.paroc.Op*, paroccipital fossa of the opisthotic; *fo.pttemp*, post-temporal fossa; I^1, first upper incisor; I_1, first lower incisor; I_2, second lower incisor; I_4, fourth lower incisor; I^5, fifth upper incisor; *Ju*, jugal; *l.r.Ang*, reflected lamina of the angular; *La*, lachyrymal; *Mx*, maxilla; *Op*, opisthotic; *Part*, prearticular; PC^1, first upper postcanine; PC^5, fifth upper postcanine; *pC*, precanine; *Pfr*, prefrontal; *Pmx*, premaxilla; *pr.c.Proot*, central process of the prootic; *pr.it.Sq*, intermediate process of the squamosal; *pr.mas.Op*, mastoid process of the opisthotic; *pr.p.-d.Op*, postero-dorsal process of the opisthotic; *pr.proot.Sq*, prootic process of the squamosal; *pr.q.Op*, quadrate process of the opisthotic; 6pr.q.Pt, quadrate process of the pterygoid, *pr.tr.Pt*, transverse process of the pterygoid; *Proot*, prootic; *Q*, quadrate; *Qj*, quadratojugal; *q.P.-Bsph*, keel of the para-basisphenoid complex; *Sang*, surangular; *Smx*, septomaxilla; *Soc*, supraoccipital; *Spl*, spenial; *Sq*, squamosal; *tub.sph.-oc, tuberculum spheno-occipitale*.

Plate III *Promoschorhynchus platyrhinus*. RC. No. 116; *A:* ventral view, the skull being slightly tilted to show the premaxillae (x 1); *B:* dorso-lateral view of the right temporal fossa (x 1); *C:* dorso-lateral view of the left temporal fossa (x 1).
a.p.Ept, posterior apophysis of the epipterygoid; *Ang*, angular; *Art*, articular; *Boc*, basioccipital; *cr.v.-it.Pt*, ventro-intermediate crest of the pterygoid; *C.s*, upper canine; *De*, dentary; *Eoc*, exoccipital; *Ept*, epipterygoid; *f.ju*, jugular foramen; *f.pt.-paroc*, pterygoparoccipital foramen; *f.v.p.*, foramen for the *vena* palatina major; *f.ven*, venous foramen; *f.vo*, vomerine foramen; *fe.ov, fenestra ovalis; fo.ipt*, interpterygoid fossa; *fo.pttemp*, posttemporal fossa; *fo.sorb*, suboribtal fossa (or suborbital vacuity); *Ju*, jugal; *La*, lachrymal; *o.ch*, internal choanae opening; *Op*, opisthotic; *P.-Bsph*, parabasisphenoid complex; *Pal*, palatine; *Part*, prearticular; *Pmx*, premaxilla; *pr.a.-d.Proot*, antero-dorsal process of the prootic; *pr.a.-v.Ept*, antero-ventral process of the epipterygoid; *pr.a.-v.Sq*, antero-ventral process of the squamosal; *pr.c.Proot*, central process of the prootic; *pr.p.-v.Ept*, postero-ventral process of the epipterygoid; *pr.proot.Sq*, prootic process of the squamosal; *pr.q.Pt*, quadrate process of the pterygoidl *pr.tr.Pt*, transverse process of the pterygoid; *Proot*, prootic; *Pt*, pterygoid; *Q*, quadrate; *q.P.-Bsph*, keel of the para-basisphenoid complex; *Qj*, quadratojugal; *Sang*, surangular; *Soc*, supraoccipital; *Spl*, splenial; *Sq*, squamosal **Tr**, transversum; *tt.orl.moy*, roof of the middle ear; *tub.sph.-oc, tuberculum spheno-occipitale; Vo*, vomer; *V2*, notch of the maxillary branch of the trigeminal nerve; *V3*, notch for the trigeminal nerve; *XII*, internal foramen of the hypoglossal nerve.

Plate IV *Promoschorhynchus platyrhinus*. RC. No. 116; *A:* anterior view (x 1); *B:* laterial view of the right epipterygoid (x 1); *C:* medical view of the left lower jaw.
a.p.Ept, posterior apophysis of the epipterygoid; *Ang*, angular; *C.s*, upper canine; *C.i*, lower canine; *cr.v.-it.Pt.dt*, ventro-intermediate crest of the right pterygoid; *Cor*, coracoid; *De*, dentary; *De.dt*, right dentary; *Eoc*, exoccipital; *f.mx*, maxillary foramen; *fo.pttemp*, post-temporal fossa; *fo.pttemp.g*, left posttemporal fossa; I^1, first upper incisor; I_1, first lower incisor; I_4, fourth lower incisor; I^5, fifth upper incisor; *Ju*, jugal; *l.d.Ept*, dorsal lamina of the epipterygoid; *Op*, opisthotic; *Pad.dt*, right palatine; *Part*, prearticular; PC^1, first upper postcanine; PC^5, fifth upper postcanine; PC_6, sixth lower postcanine; *pC*, precanine; *Pmx*, premaxilla; *pre.a.-v.Ept*, antero-ventral process of the epipterygoid; *pr.mas.Op.g*, mastoid process of the left opisthotic; *pr.p.-v.Ept*, postero-ventral process of the epipterygoid; *pr.q.Ept*, quadrate process of the epipterygoid; *pr.q.Op.g*, quadrate process of the left opisthotic; *pr.tr.Pt.g*, transverse process of the left pterygoid; *Proot*, prootic; *Sang*, surangular; *Smx*, septomaxilla; *Soc*, supraoccipital; *Spl*, splenial; *Sq*, squamosal; *Tr.g*, left transversum; *tt.orl.moy*, roof of the left middle ear; *V2*, notch for the maxillary branch of the trigeminal nerve: *V3*, notch for the mandibular branch of the trigeminal nerve; *XII*, internal foramen for the hypoglosal nerve.

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